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carpological remains, phytogeographic-climatic characterization, exotic elements, climate change, late Cenozoic, Italy

Abstract
Several terrestrial plant fossils found in the late Cenozoic of Europe belong to thermophilous genera or infrageneric taxa which do not grow in this continent today, and are usually called "exotic elements". Within this large group we singled out three more precisely defined categories based on the hypothesis that the change of geographic distribution between the late Cenozoic and the present is the result of deterministic extinctions caused by climate change. Among the taxa shared by the modern East Asian and the Plio-Pleistocene European flora, the "humid thermophilous taxa of East Asian affinity" (HUTEA) represent the central category in our study. These were traditionally considered “Pliocene” elements in Europe. In our analysis of 13 reliably dated Italian assemblages the percentage of species belonging to the HUTEA category was found to be higher in Pliocene sites, and very low to null in Pleistocene ones. Also early Pleistocene assemblages across all of Europe did not contain any HUTEA, apart from *Eucommia*, and *Glyptostrobus* and *Symplocos* sect. *Lodhra* in the refugial area of the Colchis.
Our analysis of fruit and seed assemblages in the San Lazzaro section (Umbria, central Italy), recently assigned to the early Pleistocene, provided contrasting evidence, which required a reconsideration of the stratigraphic and palaeontological context of two well known sites in central Italy, Cava Toppetti II and Dunarobba. Using vertebrate and continental mollusc biochronology the age of these sections was established and they were compared with other assemblages in central Italy and Europe. We show that in central Italy at least three HUTEA species (*Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana*) persisted after the Pliocene/Pleistocene boundary. We conclude that central-southern Italy offered a refugial niche that was warm and wet enough to assure the longer survival of some HUTEA, in contrast to central Europe.

1. Introduction

In the course of the stratigraphical and palaeontological study of the San Lazzaro section in central Italy (Fig. 1), recently assigned to the early Pleistocene (Baldanza et al., 2014), one of us (A.B.) found an endocarp of *Sinomenium cantalense*. The finding of this species, readily assignable to the humid thermophilous taxa of East Asian affinity in an early Pleistocene section was the starting point for further collecting efforts to find evidence for the role of central Italy as a centre of refuge for such thermophilous taxa in the Plio-Pleistocene (Martinetto, 2001a). In this paper we adopt the

definition of the Pliocene and Pleistocene of Gibbard et al. (2010), with the boundary fixed at 2.6 Ma, and we accept their indication for the chronologic boundaries of the four stages Zanclean, Piacenzian, Gelasian and Calabrian. Therefore, the terms middle Pliocene, late Pliocene and early Pleistocene used in previous works (among others, Ambrosetti et al., 1995a, 1995b; Abbazzi et al., 1997; Martinetto, 2001a) have a chronologic connotation which differs from that adopted here.

It is well known that many plant fossils found in the late Cenozoic of Europe belong to thermophilous genera or infrageneric taxa which do not grow in this continent today (Mai, 1989; Qian et al., 2006; Rodriguez Sanchez and Arroyo, 2008). Such fossils are usually called "exotic elements" (Reid, 1920) and this term corresponds more or less with "extinct plants" for the Plio-Pleistocene interval (Svenning, 2003). The climatic requirements are not considered in the definition of both exotic and extinct; however, several attempts have been made to assign the exotic (or extinct) elements to a few distinct plant groups that involve a climatic characterization and/or a phytogeographic aspect (Mai, 1989, 1991, 1995a; Grichuk, 1997; Grimsson et al., 2015). Examples of names which have been used include: "Palaeotropical flora/element", “Arcto-Tertiary” or “Arctotertiary flora/element” (Engler, 1879–1882; Mai, 1989, 1991; Grimsson et al., 2015), "subtropical elements" (Mai, 1970; Zagwijn, 1990), “Mastixioideen” (Kirchheimer, 1957; Mai, 1964), “Boreotropical flora” (Wolfe, 1975), “Taxodiaceae group” (Bertoldi et al., 1994), "Tethyan plants (or Tethys flora)" (Szafer, 1961; Mai, 1989; Rodriguez Sanchez and Arroyo, 2008), “Mega-mesothermic elements” (e.g. Popescu et al., 2010), "humid subtropical elements" (Bertini and Martinetto, 2011). All these names leave some uncertainty as to what is included and what is excluded from the definition, firstly because the phytogeographic information, both past and present, is superimposed to, and variously interfingers with, the climatic one, and secondly because of the very difficult, not unambiguous, climatic characterisation of the fossil-taxa (Kvaček, 2007; Grimm and Denk, 2012; Utescher et al., 2014). Also the modern reference models may be ambiguous, for example the qualitative term "subtropical" is used with very different temperature boundaries by Chinese (e.g. Hou, 1983) and Japanese authors (e.g. Kira, 1991).

The different extant distribution of plant taxa that grew together in the Cenozoic of Europe have often been given considerable relevance in the analysis of palaeofloras (see Reid and Reid, 1915; Szafer, 1961; Mai, 1964, 1989, 1995a). However, in our opinion most previous analyses and descriptions of the floral change in the Plio-Pleistocene of Europe suffered from the lack of precisely defined categories whose chronological analysis would adequately point out timing and entity of the large Plio-Pleistocene mass extinction (Tallis, 1991; Svenning, 2003). Additionally, the descriptions of Plio-Pleistocene floral changes mostly relied on pollen data (e.g. Tzedakis et al., 2006; Postigo-Mijarra et al., 2009; Magri, 2010; Orain et al., 2013), particularly in Italy (Bertini, 2010; Combourieu-Nebout et al., 2015). However, by combining pollen and carpological records (Bertini and Martinetto, 2011) it was noticed that pollen assemblages mainly reflect anemophilous plants, while they do not accurately represent the assemblages of "subtropical humid forest" type (*sensu* Hou, 1983, and Bertini and Martinetto, 2011), which are very rich in entomophilous plants and were present in southern Europe right at the time when major extinction events are hypothesized (Bertini and Martinetto, 2011). As recently confirmed by Goring et al. (2013), taxa that are pollinated by insect or animal vectors (entomophilous or zoophilous, respectively), and species with limited dispersal ability are rarely recorded in fossil pollen records. Some works on modern fruit and seed assemblages (e.g. Thomasson, 1991; Vassio and Martinetto, 2012 and references therein) indicate a less biased representation of plant diversity, in particular for several enthomophilous (e.g. *Actinidia*, *Frangula*, *Paulownia*, *Rubus*, *Sambucus*) and herbaceous plants (e.g. *Ajuga*, Cyperaceae, *Hypericum*, *Potamogeton*, etc.). For these taxa, the plant elements that enter the fossil record and allow species-level identification are fruits and/or seeds. Thus, the works which exclude carpological data definitely underestimate past plant species diversity and the extent of Plio-Pleistocene plant extinctions, and the focus of this paper will be on fossil fruits and seeds.

The analysis of the San Lazzaro material led us to reconsider the bulk of information accumulated for the Italian late Cenozoic fruit and seed assemblages in the last 30 years (in particular: Gregor,

1990; Martinetto, 1994, 1995, 1999, 2001a, 2001b, 2009, in press; Bertoldi and Martinetto, 1995; Mai, 1995b; Basilici et al., 1997; Ghiotto, 2010; Martinetto et al., 2007, 2015). Consequently, we felt the need to introduce precisely defined categories, which would permit us to better appreciate the chronological steps of the dramatic southern European floral change in the Plio-Pleistocene. One of the necessary operations was to combine in a clear manner the modern phytogeography and the climatic requirements of several taxa. Therefore, we focused on geographical and ecological characteristics of modern relatives of fossil taxa: partly shared geographic range, minimum thermic tolerance and moisture requirement. Since the geographic area where most of the "exotic" taxa of the European late Cenozoic are still living today is definitely East Asia (Tralau, 1963; Martinetto, 1998; Qian et al., 2006; Manchester et al., 2009), we considered it to be important for the definition of the new categories.

1.1. Definition of "humid thermophilous extinct European taxa of East Asian affinity" (HUTEA)

The taxonomic similarity between Neogene European floras and modern East Asian ones arerooted at least into the Miocene (Mai, 1989). As known from various studies at a global and regional scale, Cenozoic climates were generally warmer and more humid than at present, and were characterized by shallow latitudinal gradients (Utescher et al., 2011 and references therein). Several authors (Bruch et al., 2011, Liu et al., 2011, Xing et al., 2012; Jacques et al., 2013) pointed out that the climate was wetter and warmer than the present one during the Miocene in both central Europe and China. Even central and northern Eurasian areas, such as Kazakhstan (Bruch and Zhilin, 2006) and Siberia (Popova et al., 2012), were wetter and warmer during the Miocene, despite the relatively higher seasonality and continentality.

This climatic situation was probably suitable for the formation of latitudinal vegetation belts with a similar floristic composition in both western and eastern Eurasia (Mai, 1989, 1991; Kovar-Eder et al., 2008), and strong floristic affinities with East Asia have also been encountered for North American floras (Liu and Jacques, 2010). Several authors explained that the modern East Asian woody flora is richer than the European (and North American) one (e.g., Kubitzki and Krutzsch, 1996; Manchester, 1999; Tiffney and Manchester, 2001; Wen, 1999; Wen et al., 2010) mainly due to a minor impact of extinctions, even if several woody species got extinct also in East Asia during the Plio-Pleistocene (Momohara, 2015).

Some close relatives of most European extinct species were already present in the warm temperate belt of East Asia before the Pliocene (e.g., *Cathaya*, *Cephalotaxus*, *Craigia*, *Cryptomeria*, *Cyclocarya*, *Eucommia*, *Ginkgo*, *Glyptostrobus*, *Pseudolarix*, *Taiwania*: Manchester et al., 2009) or possibly migrated there during the Pliocene (e.g., *Hemiptelea*, *Rehderodendron*: Manchester et al., 2009), and could survive the Pleistocene climatic crisis because of the presence of niches that were wet (atmospheric humidity) and warm enough, even in sites not related to rivers and swamps. Based on the concept of "physiological uniformitarianism" (Tiffney and Manchester, 2001) we can assume that the climatic tolerances of the living relatives of Neogene European taxa that survived in the humid and warm temperate to tropical areas of East Asia roughly correspond (maybe only in part) to those of the extinct European forms of the same genus, subgenus or section. Svenning (2003) pointed out a deterministic effect in late Cenozoic plant extinctions and recognized three important groups of taxa for the analysis of the ancient European floras: 1) widespread taxa; 2) relictual taxa; 3) extinct taxa. In referring to extinct taxa, Svenning (2003) restricted his analysis to cool-temperate tree genera, but recently Eiserhardt et al. (2015) carried out an analysis on more thermophilous plants. Actually, several Plio-Pleistocene taxa occurring in Europe are more thermophilous than “cool-temperate” (Martinetto et al., 2015) so that we now consider it important to single out a new group of thermophilous taxa with a partly shared (as for eastern Asia) current distribution outside Europe and a common, definite climatic boundary. The thermophilous characterization of several taxa documented by fossils is provided by the minimum Mean Annual Temperature (MAT) requirement of their modern relatives (Table 1).

Consequently, we define as "**HU**mid **T**hermophilous extinct European taxa of **E**ast **A**sian affinity", in short HUTEA, those plant taxa which have well-documented fossil records in the late Cenozoic of Europe, which do not grow spontaneously in this continent and West Asia at present (unless as aliens), which do not tolerate a Mean Annual Temperature below 8°C and a Mean Annual Precipitation (MAP) below ca. 800-1000 mm/year, and which belong to genera or infrageneric taxa that presently grow in East Asia (Wang, 1961; Qian et al., 2006; Manchester et al., 2009; Fang et al., 2009, 2011; Grimm and Denk, 2012; Eiserhardt et al., 2015; Utescher and Mosbrugger, 2015).
We single out the 8°C value of MAT because this is the boundary of the distribution of boreal (subarctic) and thermophilous (temperate) taxa in East Asia. The lower limit of fir and spruce forest and the upper limit of deciduous forest is 7.8 °C MAT in China (Fang and Yoda, 1989). Although the lower MAT limit of the thermophilous evergreen arboreal Fagaceae and Lauraceae (dominant tall trees of temperate broadleaved evergreen forests in East Asia) is between 9 and 12°C (Hattori and Nakanishi, 1985; Fang and Yoda, 1989; Fang et al., 2011), we decided that adding 1°C of tolerance would admit sporadic occurrences of thermophilous plants above the 9°C MAT isotherm.
The focus on MAT for the definition of the HUTEA is justified by the large availability of data (Grimm and Denk, 2012; Utescher and Mosbrugger, 2015) for most of the plant genera documented by fossils in Europe, and by the determinant role of this parameter for plant extinction or survival in the late Cenozoic of Europe (Svenning, 2003; Eiserhart et al., 2015). Conversely, we did not manage to gather precise values of minimum precipitation requirements for all the exotic Neogene plant taxa of Europe; nevertheless we consider important to include in the HUTEA definition a rule that excludes those plants which tolerate a low precipitation (below ca. 800-1000 mm/year). In fact it has been pointed out that the extinction of several Neogene taxa in Europe dependended from a scarce tolerance not only of low temperature, but also of low precipitation (Svenning, 2003; Eiserhart et al., 2015). The thermophilous genera that survived in southern Europe until present time (e.g. *Laurus*, *Olea*) are mainly adapted to dry (Mediterranean) climate, whereas several thermophilous genera extinct in Europe are now growing in areas affected by the East Asian Monsoon that supplies higher precipitation to plants during the growing season. In East Asia the main evergreen forest formation, dominated by Fagaceae and Lauraceae, is called “lucidophyllous forest” and differs from the south European (Mediterranean) sclerophyllous forest formation by its less xeromorphic characteristics, such as larger shiny leaves, larger tree size and higher species diversity with many epiphytes and woody lianas (Kira, 1991).
We are aware that other parameters (e.g. Warmth Index, Coldness Index; Kira, 1991) could be more appropriate to define a category such as HUTEA. Nevertheless, the minimum MAT requirement is an important factor determining the possibility for a plant taxon to overcome a climatic bottleneck. The climatic characteristics of the refugia might have been been decisive for the possibility of a plant species to survive (Magri, 2010; Gavin et al., 2014) and obviously it would have gone extinct if its minimal thermal or humidity requirements would no longer have been present in the last refugium. In this respect, groups of taxa with similar requirements may be expected to go extinct together (Tallis, 1991; Grichuk, 1997; Eiserhardt et al., 2015). However, some extinctions are certainly controlled by complex and multiple factors. For example it has been suggested that *Cedrus* (Su et al., 2013) and *Sequoia* (Zhang et al., 2015) disappeared from China because of seed ecological aspects, triggered by climate change.

Three examples, concerning genera which do not tolerate a MAT below 8°C (Table 1), may be useful to support the above definition of HUTEA: *Toddalia* is assigned to the HUTEA because it is distributed in the tropical-warm temperate zone of East Asia and in Africa, but not in Europe and West Asia (Gregor, 1979). *Symplocos* sect. *Lodhra* is assigned to the HUTEA because it is distributed in the tropical-warm temperate zone of East Asia, but not in Europe and West Asia (Fritsch et al., 2015). *Rehderodendron* is assigned to the HUTEA because it is distributed only in the “subtropical” zone (*sensu* Hou, 1983) of East Asia.

The genera *Cathaya* and *Pseudolarix* meet all the requirements to be classified as HUTEA, but they are excluded for their present highly relictual distribution, which may provide an inaccurate representation of their past climatic requirements, similarly as for *Tetraclinis* (Kvaček, 2007). *Azolla* is not considered a HUTEA because it is a water plant rather independent from atmospheric humidity.

(TABLE 1 approximately here)

According to the above definition and to the data (e.g., minimum thermic requirements: MATmin) reported in Table 1, the following HUTEA have so far been documented for the late Cenozoic of Italy (Martinetto, 1995, 1998, 1999, 2001a; 2001b; Follieri, 2010; Martinetto et al., 2015): *Amentotaxus*, *Cephalanthus*, *Cinnamomum*, *Craigia*, *Cyclea*, *Cyclocarya*, *Ehretia*, *Engelhardia*, *Eucommia*, *Glyptostrobus*, *Mallotus*, *Meliosma* subgen. *Kingsboroughia*, *Paulownia,* *Rehderodendron*, *Sabia*, *Sargentodoxa*, *Saurauia*, *Sinomenium*, *Stemona*, *Symplocos* sect. *Lodhra*, *Taiwania*, *Ternstroemia*, *Tetrastigma*, *Toddalia*, *Trichosanthes*, *Turpinia* and *Wikstroemia*.

1.2. Other categories (CTEA, TEWA)

Other taxa documented in the late Cenozoic of southern Europe have the correct geographic distribution nowadays to be considered HUTEA (i.e. embracing East Asia and excluding Europe and West Asia), but they are not considered, because the modern representatives do tolerate a Mean Annual Temperature below 8°C (e.g. *Actinidia*, *Alangium*, *Ampelopsis*, etc.: Table 1). These taxa will be named CTEA ("**C**ool-**T**olerant extinct European taxa of **E**ast **A**sian affinity") in this paper and belong to the somehow ambiguous [changing on the basis of the extent of territory considered] category of the "exotic" taxa (Reid, 1920; see the more precisely defined "category E" in Martinetto, in press).

The HUTEA category already has a satisfactory climatic connotation, which we deem to be useful for an analysis of the climatic determinism in their extinction. Conversely, the CTEA category certainly contains a very heterogeneous mix of species with different climatic tolerances. In fact, *Magnolia* provides a good example of a cool-tolerant CTEA genus that contains several modern species (Grimm and Denk, 2012; Mosbrugger and Utescher, 2015), which are absolutely thermophilous and not cool-tolerant (tropical-subtropical). Similarly, a diversified climate tolerance has been also hypothesized for different European fossil-species (Mai, 1975). Given this situation, it is not surprising that several CTEA would show a HUTEA-like extinction pattern. However, in this paper our attention has been focused on the species that show a delayed disappearance time in comparison to the HUTEA.

Finally, a few taxa which do not tolerate a MAT below 8°C are not assigned to the HUTEA because of the modern geographic range: *Coriaria*, *Datisca*, *Ficus*, *Laurus*, *Liquidambar*, *Morella*, *Ocotea*, *Olea*, *Platanus*, *Sideroxylon*, *Styrax*, *Tetraclinis* and *Visnea* grow in southern Europe, North Africa (incl. Macaronesia) and/or West Asia. These taxa will be indicated as TEWA, **T**hermophilous **E**uropean, **W**est Asian and/or **A**frican elements, in this paper. *Pterocarya*, *Parrotia* and *Zelkova* are not assigned to the HUTEA nor to the CTEA or TEWA, because they grow in relict niches of south-eastern Europe and/or West Asia (southern shores of the Black Sea and Caspian Sea), commonly including sites with a Mean Annual Temperature below 8°C.

Finally, late Cenozoic south European taxa that today only survive in America are not many (*Decodon*, *Dulichium*, *Leitneria*, *Proserpinaca*, *Sequoia*, *Taxodium*) and will not be specifically dealt with in this paper.

It is apparent that the HUTEA and CTEA concepts have much to do with a change of geographic distribution between the Plio-Pleistocene and the present. The main aim of this work is to present new fossil data from Italy and an updated state-of-the-art regarding the timing of disappearance of

HUTEA and CTEA species from Europe. Furthermore, we newly consider the possibility of deterministic extinctions (Svenning, 2003; Eiserhardt et al., 2015).

2. Geological setting

The post-Miocene, NW-SE oriented South Valdichiana Basin (Fig. 1), enclosed between the Meso-Cenozoic Rapolano-Mt. Cetona and Narnese-Amerina Apennine anticlines and bounded by extensional faults, occupies a wide area between south-eastern Tuscany and western Umbria, in central Italy. In the Pliocene-Pleistocene interval, the Narnese-Amerina ridge separated the mainly marine domain of South Valdichiana from the continental deposits of the Southern Tiberino Basin (Figs. 1, 2), while, during the early Pleistocene, a wide delta in what is now the Città della Pieve area divided the continental (northwards) and the marine Valdichiana (southwards) (Bizzarri and Baldanza, 2009; Bizzarri et al., 2015).

(FIGURE 1 approximately here)

South Valdichiana marine deposits in the study area, including the San Lazzaro section (Fig. 1), clearly mark a regressive trend, from offshore transition silty sands to lower shoreface sands, and finally to a gravel beachface with evidence of a river mouth in the uppermost part (Baldanza et al., 2011). The same main trend is recognized in other sections nearby, such as the Monteleone section and the Città della Pieve section (Bizzarri and Baldanza, 2009). All these sections are referred to alternatively river- and wave-dominated shallow coastal marine environments (Bizzarri et al., 2015), and attributed to the “Deltaic coast” inside the “Chiani-Tevere” Unit (Fig. 2, Baldanza et al., 2014; Martinetto et al., 2014). On the other hand, through late Pliocene and early Pleistocene, the Southern Tiberino Basin evolved from a wide lacustrine environment to a river-drained valley system (Ambrosetti et al., 1995a; Basilici, 1997, 2000a, 2000b; Martinetto et al., 2014). The sections Cava Toppetti II (Abbazzi et al., 1997) and Dunarobba (Ambrosetti et al., 1995b) are representative of this second context.

(FIGURE 2 approximately here)

3. Materials and methods

This work integrates the analysis of freshly collected material from the San Lazzaro section with the reinterpretation of the stratigraphic and palaeontological data from the sites Cava Toppetti II (Abbazzi et al., 1997; Argenti, 1999, 2004; Martinetto, 2001a; Petronio et al., 2003; Sardella et al., 2003) and Dunarobba (Ciangherotti et al., 1998; Manganelli and Giusti, 2000; Manganelli et al., 2008; Martinetto et al., 2014).

In the San Lazzaro section, as well as in the neighbouring sections (Fig. 3), a close, about 1 m spaced, sampling for marine microfossils ("biostratigraphic samples") was carried out in the lowermost deposits, in order to provide an integrated biostratigraphical datum. Similarly, more widely spaced biostratigraphic samples were collected in the upper part of the section, in correspondence of fine-grained deposits. For each sample, 100 g of sediment were processed with H_2O_2 solution, washed through a 63 μ size mesh, and the residue observed using a stereomicroscope. Smear slides for nannoplankton analysis were prepared using the standard technique proposed by Bown and Young (1998), and observed under a polarizing-light microscope at 1000x magnification.

(FIGURE 3 approximately here)

The above-mentioned finding, in a biostratigraphic bulk sample (FU6, ca. 100 g) collected at 14 m, of a fruit part (endocarp) of *Sinomenium cantalense* was the starting point for a more extensive sampling effort in the San Lazzaro section. A few concentrations of compressed plant fragments were noticed in the portion from 5.5 m to 8.5 m of the section (Fig. 4), and three bulk sediment samples FU3 and FU4, ca. 400 g, and FU5, ca. 2000 g; these are named "carpological samples") have been collected there and processed with the palaeocarpological method illustrated in Basilici et al. (1997).

The methods for the identification of plant materials are the same as those recently described in Martinetto et al. (2015). However, the climatic characterisation of each plant fossil-species was

carried out differently. We did not use only the data available in the Paleoflora Database (PFDB: Utescher and Mosbrugger, 2015) and in the GrimClim Database (CG: Grimm and Denk, 2012), because these data have several biases depending from their literature sources: the PFDB does not indicate references for the thermal boundary values referred to each taxon, and the boundary temperatures of Fang (2011), largely used by the CG, were defined from very rough distribution data at county level (several Chinese provinces are larger than Japan). Therefore, whenever possible, we used in Table 1 the more precise data from different literature sources (Alternative MATmin in Appendix 1). Those include local floras and vegetation survey reports in China and Japan, in which distribution of taxa are described and/or mapped on the altitudinal scale of at least 100 m based on herbarium specimens and/or field observations (Appendix 1).

(FIGURE 4 approximately here)

Deposits in the area of Fabro Scalo (Fig. 1) have been investigated with the aim to: 1) reconstruct a lithostratigraphic section for the area, 2) better document the palaeofloral assemblages inside the phytodebris-rich horizons of the San Lazzaro outcrop, 3) establish the age of these deposits, and 4) compare the plant assemblages with other possibly coeval assemblages in central Italy, first of all those of the dated Cava Toppetti II section (Abbazzi et al., 1997; Martinetto, 2001a), and secondly those of poorly dated Dunarobba succession (Martinetto et al., 2014). To reevaluate the age of these three sections, data on vertebrate and continental mollusc biochronology were reconsidered (Abbazzi et al., 1997; Gliozzi et al., 1997; Ciangherotti et al., 1998; Petronio et al., 2003; Sardella et al., 2003; Argenti, 2004; Manganelli et al., 2008).

In addition, continental mollusc and vertebrate records were investigated as complementary palaeoclimatic evidence to terrestrial plants. In particular we analysed the history of the HUTEA plants in parallel with that of the terrestrial ectothermic vertebrates, whose distribution is clearly related to historical variations of temperature and humidity more directly than that of other vertebrates (Delfino, 2002; Kotsakis et al., 2004; Venczel and Sanchiz, 2005; Delfino et al., 2006; Delfino and Sala, 2007; Piras et al., 2007; Delfino et al., 2008).

Even if we base our analysis on the climatic determinism of plant extinctions, the correlation of the disapperance events with the standard climatic curves (e.g. Zachos et al., 2001; Lisecki and Raymo, 2005; De Shepper et al., 2013; Prescott et al., 2014) requires more information and is beyond the scope of this work.

3.2. Carpological and floristic analyses

The San Lazzaro sediment samples FU3, FU4 and FU5 were prepared according to a standard palaeocarpological method (Martinetto, 1994; Basilici et al., 1997). The definition of the HUTEA category allowed us to carry out a new floristic analysis, both for the San Lazzaro assemblage and for several other Pliocene and early Pleistocene floras of Italy: we selected 13 reliably dated assemblages (2 of the Zanclean, 5 of the Piacenzian, 2 of the Gelasian, 3 Calabrian, 1 early Middle Pleistocene) and we analysed the percentage of species belonging to the HUTEA category, referred to the total number of species (Table 2). Furthermore, since our focus was on the early Pleistocene, we also analyzed the floral lists of all the main carpofloras of the rest of Europe (Baas, 1932; Chochieva, 1965; Buzek et al., 1985; Mai and Walther, 1988; Günther and Gregor, 1990; Velichkievich and Zastawniak, 2003; Mai and Velitzelos, 2007) whose age was proved or supposed to fall within that time interval (Table 3).

(TABLE 2 approximately here)

(TABLE 3 approximately here)

In order to get an overview of the disappearance times of themophilous plants at the south European scale, the occurrence and suggested extiction time of HUTEA were also checked in synthetic

palynological papers dealing with the following areas: whole area (Popescu et al., 2010), Iberian peninsula (Postigo-Mijarra et al., 2009), Italy (Bertini, 2010; Magri, 2010; Combourieu-Nebout et al., 2015), Balkan Peninsula (Tsedakis et al., 2006; Biltekin et al., in press), Colchis area (Shatilova et al., 2014) and Turkey (Biltekin et al., in press).

4. Results

4.1. The San Lazzaro section and its age constraints

The composite sedimentological and stratigraphic reconstruction proposed for the Fabro Scalo area integrates old observations (Baldanza et al., 2011, 2014; Bizzarri et al., 2015) and newly collected data. The general geological and sedimentological pattern, from the base to the top, is organized as follows (Fig. 3):

- about 10 m (cropping out) of structureless, mollusc-rich clayey and silty sand (offshore transition deposits); the lowermost layers are covered by recent alluvial deposits;
- up to 30-40 m of highly fossiliferous (mainly molluscs) fine sand (lower shoreface deposits);
- up to 25 m of intermingled coarse sand and gravel (gravel beachface deposits);
- a minimum of 20 m of channelled gravel with minor sand (river mouth deposits).

The about 27 m-thick San Lazzaro section represents approximately the lower/intermediate part of this composite section (Fig. 3); deposits grade up from poorly sorted silty sand, referred to the offshore transition, to moderately sorted fine sand of lower shoreface. Throughout the section, a rich and diversified fossil record (Baldanza et al., 2014; Bizzarri et al., 2015), dominated by molluscs, echinids, lunulite bryozoans, benthic foraminifera and decapod crustaceans was documented; both macro- and micropaleontological assemblages are dominated by benthic taxa, mostly referred to warm shallow water conditions.

As for the Monteleone and the Città della Pieve sections, deposits in the Fabro Scalo area are mainly referred to the MNN 18 - MNN 19a zones (*sensu* Rio et al., 1990) on the basis of nannofossil assemblages: rare small-sized *Gephyrocapsa* spp. (*sensu* Raffi, 2002), *Helicosphaera sellii*, *Calcidiscus macintyrei*, very rare and broken *Discoaster brouweri* and *Coccolithus pelagicus*. Trough the composite lithostratigraphic section, two calcareous nannofossil biostratigraphic events are recognized (Fig. 3): the LO of *Discoaster brouweri* (top of MNN 18 zone, t*Db sensu* Raffi, 2002) in the lowermost part of the Fabro-Carnaiola section, and the FO of medium-sized *Gephyrocapsa* spp. (base of MNN19b subzone, b*mG sensu* Raffi, 2002) at about the top (22 m) of the San Lazzaro section. Therefore, the biostratigraphic data permit to assign deposits to the Gelasian *pro parte* - Calabrian *p.p*. interval. This transition is also marked by the occurrence, in the lowermost deposits, of marine ostracods such as *Aurila cruciata*, *Loxoconcha glabra*, *Argilloecia* sp., and *Ruggieria longecarenata*, usually documented from the end of the Gelasian and the base of the Calabrian (Faranda and Gliozzi, 2008). The occurrence, throughout Gelasian-Calabrian sections, of taxa of previously supposed "Pliocene affinity", such as *Amphistegina* spp. and *Persististrombus* cf. *coronatus*, is not surprising, nor sufficient to suggest an older (Piacenzian) age: in fact, the persistence of these taxa into Gelasian to Calabrian deposits has been documented in other sites of this area (Bizzarri and Baldanza, 2006; Monaco et al., 2011). The two horizons with carpological remains, inside the San Lazzaro section (Fig. 3), are attributed to the MNN 19a subzone, well inside the early Pleistocene, and are still referable to the Gelasian stage.

4.1.1. The San Lazzaro carpological assemblage

The preparation of the San Lazzaro carpological samples yielded plant assemblages mainly made up of woody fragments, particularly abundant in sample FU5. However, a careful observation allowed us to separate also a few, mostly fragmentary, fruits and seeds. Samples FU3 and FU4 had a very poor carpological content, reported in Table 4, whereas FU5 yielded more abundant carpological material that allowed us to identify five definite fossil-species (ICN, McNeill et al.,

2012) well-known in the Pliocene of Italy (see Table 4 for the number of specimens): *Magnolia allasoniae*, *Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana* and *Zanthoxylum ailanthiforme*. The occurrence of 3 HUTEA out of 6 species forming the San Lazzaro plant assemblage (Table 4) represents a very high percentage (50%). So, the precise identification at species level allowed by fruit morphology give to these few remains a relevant importance, due to the stratigraphic context in which they have been found. These taxa have been described and figured in Martinetto (2001a, 2001b), Mai and Martinetto (2006) and Martinetto et al. (2014, 2015). A single species has been left in open nomenclature for the reason discussed below:

- *Vitis* cf. *vinifera* L. subsp. *sylvestris* Gmelin - seeds of *Vitis* with distinct similarities to the modern Mediterranean wild grape *V. vinifera* subsp. *sylvestris* are abundant in several tens of Italian fossil sites spanning from the Zanclean to the Holocene (Martinetto, 1994; Basilici et al., 1997; Cavallo and Martinetto, 2001). However, their assignment to the modern species (and subspecies) is not straightforward because a similar fossil-species has also been described (*Vitis parasylvestris* Kirchheimer 1957) and often reported in the Neogene of Europe (Geissert et al., 1990; Martinetto, 1994; Mai, 2001). The diagnostic features of this last species are said to be the length up to 7 mm and the small seed body associated to a narrow cylindrical basis, somehow similar to that of the Holocene cultivated forms of *V. vinifera* subsp. *vinifera*. The consistent variability of morphological characters observed in rich fossil populations makes a precise assignment at species level problematic, in the absence of a detailed statistical and morphometric study. However, the dimensions and the shape of the base in the Plio-Pleistocene Italian seeds is mostly the same as in the modern Mediterranean species, so that a major affinity to *Vitis vinifera* subsp. *sylvestris* than to *V. parasylvestris* is suggested also for the specimen of San Lazzaro.

(TABLE 4 approximately here)

4.1.2. Taphonomical considerations

Almost the whole carpological record of San Lazzaro comes from a thin lens of mixed shells and compressed phytodebris (FU5 in Table 4). Several lenses of this type are usually well exposed and recognizable after periods of intense rain (Fig. 5). Each lens is concave upwards, up to 40 cm wide, less than 10 cm thick, and filled by structureless clastic-bioclastic very fine sand, just a little coarser than the enclosing silty sand deposits. Mollusc shells and fragments are usually found at the bottom or in the lateral parts, while thin wood fragments are more randomly dispersed. In the 4-9.5 m interval (Fig. 3), such lenses are frequent, interposed to both shell lags and spotted mollusc specimens. Millimetric, isolated wood fragments (compressions) are locally spread through the rest of the section. A speditive anatomical analysis (stereomicroscope) proves that most of the phytodebris consists of heteroxylous and homoxylous xylem fragments, thus proving their origin from terrestrial or at least coastal woody plants. The abundance of such plant remains in a shallow marine nearshore environment probably reflects river flood events from neighboring areas. Distally, from the prodelta to the offshore marine environment, major events may trigger remobilization of sediments (sediment-gravity flows *sensu* Lowe, 1982 and Nemec and Steel, 1984), including density currents (turbidity currents). Several plant fragments horizons inside massive to laminated sandy sediments are interpreted as part of turbidites *s.l.* and even diagnostic of hyperpycnal flows (hyperpycnites: Zavala et al., 2012). On the other hand, the San Lazzaro deposits were referred to lower shoreface/offshore transition by means of sedimentological features (Baldanza et al., 2014; Bizzarri et al., 2015), and no evidences of deposits related to turbidity currents and/or hyperpycnal flows was found. Thus, the depositional models proposed by Zavala et al. (2012) to account for the richness of plant remains, leaves, charcoal or other very light land-derived materials in distal to deep marine deposits cannot be applied here. As well as the shell lags, these lenses can be interpreted as storm layers: plant remains transported to the sea during intense floods (in mass transport) by small rivers, depending on their size and density, may more or less longer float or quickly settle to the seafloor. As for other bioclasts, woody fragments and even larger branches and

trunks (Monaco et al., 2011) are remobilized during storm events, and redistributed inside storm layers. The small dimensions of fragments (up to few centimetres, usually <1 cm), the lack of whole leaves, the partially abraded aspect of carpological remains, their concentration inside lenses of very fine sands, surrounded by silty sand-dominated deposits, all indicate discontinuous, wave-induced sedimentation events (tempestites) in a relatively low energy environment. The possibility of reworking of plant material in marine environments was already discussed in Martinetto et al. (2015).

(FIGURE 5 approximately here)

4.2. The Dunarobba section

An updated overview of the stratigraphic information on several sections of the Dunarobba site can be found in Martinetto et al. (2014), and here we concentrate on two types of rich and well-diversified molluscan assemblages from the Dunarobba Forest Section (DF). The first, coming from the silty clays encrusting the trunks, is dominated by extinct hygrophilous land prosobranchs and pulmonates, such as *Hydrocena dubrueilliana*, *Carychium* (*Saraphia*) *pachychilum*, *C.* (*S.*) *pseudotetrodon*, *Negulus villafranchianus*, *Leiostyla gottschicki*, *Gastrocopta* (*Albinula*) *acuminata fossanensis* (= *G.* (*A.*) *acuminata*), *Gastrocopta* (*Vertigopsis*) *dehmi* (= *G.* (*V.*) *moravica*), *Eostrobilops aloisii*, *Staurodon cianfanellianus*, *Laminifera* (*Laminiplicata*) *villafranchiana* (= *Laminiplica villafranchiana*) (Manganelli et al., 1989, 1990; Esu and Girotti, 1991, Esu et al., 1993; Ciangherotti et al., 1998; Manganelli and Giusti, 2000; Manganelli et al., 2008). These species are of high palaeobiogeographical and biochronological interest. Most of them, such as *H. dubrueilliana*, *C. pseudotetrodon*, *N. villafranchianus*, *G.* (*V.*) *dehmi* (= *G.* (*V.*) *moravica*), *G.* (*A.*) *acuminata fossanensis* (= *G.* (*A.*) *acuminata*), *L. gottschicki*, *E. aloisii*, *L. villafranchiana*), are in common with the NW Italian assemblages of the late Pliocene (Piacenzian of the marine chronostratigraphy) deposits of Villafranca d'Asti (RDB section) or Ceresole d'Alba and other Pliocene sites (Ciangherotti, 1997; Esu and Ciangherotti, 2004, Ciangherotti et al., 2007), and mostly got extinct during the late Pliocene (Piacenzian)/early Pleistocene (Gelasian) transition.

The second assemblage, coming from the sediments around the trunks of the Forest Section (Martinetto et al., 2014), is characterized by aquatic prosobranchs, such as *Theodoxus groyanus, Emmericia umbra, Prososthenia paulae, Tournouerina belnensis, Melanopsis affinis, Micromelania* (*Goniochilus*) *zitteli,* mainly endemic to central Italy and getting extinct in the late early Pleistocene (Ambrosetti et al., 1995b; Ciangherotti et al., 1998; Esu and Girotti, 2001).

Thanks to a high percentage of extinct molluscs of Pliocene character and to the findings of land species common to the late Pliocene molluscan fauna of NW Italy and other European Pliocene sites, it is possible to suggest a late Pliocene age (Piacenzian) for the Dunarobba molluscan fauna, even if a late Pliocene-earliest Pleistocene age (Piacenzian-Gelasian) cannot be excluded. The climatic indications of these molluscs, based on the modern relatives, indicate a warm temperate climate with a high atmospheric humidity, e.g. the genus *Eostrobilops* lives in East Asia, South of 40° N, and *Negulus* in East Africa (Ethiopia) (Esu and Ciangherotti, 2004).

The occurrence of several fruit and seed assemblages in different sections of the Dunarobba site has been recently reported by Martinetto et al. (2014). The most diverse plant assemblage, originating from a sandy bed indicated as DC1b, included 41 species, 8 of which are recognized as HUTEA with a resulting percentage of 20%.

4.3. The Cava Toppetti II section

The Cava Toppetti site, a few kilometers south-west of Todi (Fig. 1), was comprehensively investigated during the two last decades, and several sedimentological, stratigraphic, palaeontological and palaeoenvironmental data were collected (Ambrosetti et al., 1995a; Basilici, 1995; Abbazzi et al., 1997; Gliozzi et al., 1997; Pontini, 1997; Leone et al., 2000; Pontini et al., 2002; Martinetto et al., 2014). Due to the presence of two completely different successions, cut through by a main extensional fault, the various records were referred to either Cava Toppetti I, the older succession made up by the Fosso Bianco Unit (FBU), or Cava Toppetti II, the younger

succession made up by the Ponte Naja Unit (PNU). Both the FBU and PNU (Fig. 2: Ambrosetti et al., 1995a; Basilici, 1995) were well exposed through the quarry fronts in the 1980s-1990s, but later the outcrop was deteriorated by the lack of quarrying activities, the successive backfilling and the slope restoration.

(FIGURE 6 approximately here)

The about 150 m thick Cava Toppetti II section pertained to the uppermost PNU; it was composed (Fig. 6) of prevailing clayey-sandy silt deposits (fine-grained sheet flow deposits), with interposed silty clay (palaeosol), planar-concave sandy gravel (stream ribbon channels) and tabular sandy gravel deposits (coarse-grained sheet-flow deposits). A complete sedimentological description and interpretation of PNU deposits can be found in Basilici (1995) and Abbazzi et al. (1997). The palaeoenvironment was reconstructed on a sedimentological basis as the medial and distal portion of an alluvial fan. Several types of sediments locally bear molluscs, whereas fragments of large vertebrates and micromammals were mainly collected inside palaeosols. According to Abbazzi et al. (1997), deposits of Cava Toppetti II section originally overlie the about 300 m thick lacustrine laminated silty clay deposits of the FBU, attributed to late Pliocene-early Pleistocene by means of magnetostratigraphy (Late Gauss to Early Matuyama Chrons).

At Cava Toppetti II an important biochronological datum is given by the occurrence of the micromammal *Apodemus dominans* (Argenti, 1999; Sala and Masini, 2007). In the southwestern branch of the Tiberino Basin such occurrence has been recorded also at the Pantalla site, together with a diversified vertebrate assemblage (Gentili et al., 1997; Cherin et al., 2013a, 2013b, 2014a, 2014b). All the vertebrate data support a biochronological framework with Cava Toppetti II and Pantalla referable to the middle-late Villafranchian transition (Coste San Giacomo or Olivola Faunal Units), i.e. to the late Gelasian (Cohen et al., 2013). Recently, Bellucci et al. (2014) provided new data on the Coste San Giacomo faunal assemblage, including also small vertebrates. The age of this deposit, reference locality of the Coste San Giacomo Faunal Unit, has been approximately assessed at 2.1 Ma. The ongoing researches will allow a more detailed comparison of the Cava Toppetti II mammal assemblage to those of Coste San Giacomo and of the other Umbrian localities mentioned above.

The molluscs collected in the alluvial fan deposits of the Cava Toppetti II section (Abbazzi et al., 1997) are characterized by a few extinct freshwater prosobranchs, such as *T. groyanus*, *E. umbra*, *Choerina tudertis*, *M. affinis*, *Prososthenia augusti, P. tassoi*, which are endemic to central Italy, and by a few extinct species of land snails, such as *Carychium* (*Carychiella*) *puisseguri*, *Carychium* (*Saraphia*) *pachychilum*, *Carychium* (*S.*) *pseudotetrodon* and *Negulus villafranchianus*. Among these, only three species are shared with the Dunarobba assemblage, whilst all the species of freshwater prosobranchs were recovered also at Dunarobba. The PNU land molluscan fauna results impoverished in extinct molluscs compared with the Dunarobba one indicating a slightly younger age, that is early early Pleistocene (Gelasian). The lack of most of the thermophilous taxa occurring at Dunarobba, such as the representatives of the genera *Hydrocena*, *Eostrobilops*, *Staurodon*, *Laminiplica*, suggests a cooler climate during the deposition of the PNU unit in comparison to the Dunarobba Fossil Forest one (Ciangherotti et al., 1998). Furthermore, these taxa are also less exigent in terms of atmospheric humidity.

As for the macroscopic plant remains, the record of the Cava Toppetti II section is rather poor, but an important fruit and seed-bearing deposit (Fig. 7) has been located in the middle part of the section (Fig. 6) and the occurrence of several species had been reported by Martinetto (2001a). As a whole 40 species have been identified, 8 of which are recognized as HUTEA with a resulting percentage of 7%.

(FIGURE 7 approximately here)

All the data presented above call for a rconfirmation of the chronological position of the Cava Toppetti II section. We know that some recent papers challanged the reliability of several old

paleomagnetic data, due to some bias on magnetic minerals (e.g. the issue related to the Jaramillo subchron discussed in Muttoni et al., 2014). However, the bulk of data collected in the Tiberino Basin, their correlation with part of the Valdarno Basin sequence, which is also time-calibrated by means of radiometric data (Bertini, 2013), and the magnetic susceptivity-based high-resolution cyclostratigraphy (Pontini et al., 2002; Napoleone et al., 2003, 2004), make the chronologic interpretation of the Cava Toppetti II succession reliable in the light of current knowledge. Thus, on the basis of its palaeontological content and stratigraphic position, the section is thought to be early Pleistocene (Gelasian) in age, younger than the Reunion Event and older than the Olivola Faunal Unit, which is placed at the end of the normal polarity subchron Olduvai (Torre et al., 1996; Napoleone et al., 2003; Bellucci et al., 2014). The sedimentological features suggest a high sedimentation rate (>1.3 mm/y: Basilici, 1995; Abbazzi et al., 1997), and a time span of about 100 ky to 300 ky is presumed for the whole Cava Toppetti II section, inside the 2.1-1.9 Ma range; (Abbazzi et al., 1997; Leone et al., 2000; Martinetto et al., 2014).

4.4. Frequency of the HUTEA since 5 Ma and last occurrence of CTEA

The percentages of species belonging to the HUTEA category in the well-dated reference floras of Italy (Fig. 8, Table 2) show that the Zanclean-Piacenzian assemblages have a higher value (7-31%), and the HUTEA are constantly present in all the floras that are well dated within this time interval, and also in those tentatively assigned to it (Martinetto et al., 2015; Martinetto, in press). A single HUTEA (*Eucommia*) occurs in one (Arda-AD3) of the two Gelasian reference assemblages (2% HUTEA), whereas the other Gelasian assemblage (Casnigo) and all of the Calabrian-Middle Pleistocene ones are devoid of HUTEA. Also the main European carpofloras definitely or possibly dated to the Gelasian-Calabrian would be devoid of HUTEA (Table 2), if not for the occurrence of *Eucommia* at Tegelen and Schwanheim.

Another late occurrence of two HUTEA species has been reported for a fossil flora of the Colchis area (Kvarbeti, Georgia): *Glyptostrobus europaeus* and *Symplocos casparyi* (*Symplocos* sect. *Lodhra*). This flora was referred by Chochieva (1975) to the Gurian local stage, which is now correlated to the Calabrian (Shatilova et al., 2014). Biltekin et al. (in press) even suggest the persistence of *G. europaeus* in the Holocene of the southern Black Sea.

(FIGURE 8 approximately here)

Our newly recovered Gelasian assemblage of San Lazzaro, with 50% HUTEA, is an exception at the European scale, but it must be considered that the low number of species may have biased this value. The other Gelasian assemblage available in central Italy, Cava Toppetti II, has 7% HUTEA and the Piacenzian or Gelasian Dunarobba assemblage has 20% HUTEA. These floras, similar to other Gelasian-Calabrian ones of Italy (Girotti et al., 2003, Martinetto, 2001a; Martinetto et al., 2015) and Europe (Table 2) are still very rich in CTEA, commonly associated with *Parrotia*, *Pterocarya* and *Zelkova*. By merging the occurrence data of HUTEA (Fig. 9), CTEA (compare Table 1 with data in Martinetto, 2001a, and Martinetto et al., 2015) and TEWA (Martinetto, 2001a; Martinetto et al., 2015) it is apparent that at least 70 plant species disappeared from southern Europe in the time interval between latest Zanclean (3.7 Ma) and early Middle Pleistocene (0.5 Ma).

(FIGURE 9 approximately here)

4.5. Ectothermic vertebrate record (amphibians and reptiles)

The Italian peninsula hosted in the past a few reptile genera that went locally extinct (with a timing different from that of the HUTEA) and now survive in a stripe that extends eastward from the Balkan Peninsula to Indonesia, but still preserves in an exclusive way some amphibians that once had a much larger range. Examples are *Agama s.l.*, *Pseudopus*, *Tomistoma*, *Vipera* (oriental group), among thermophilous reptiles (Delfino, 2002; Kotsakis et al., 2004; Piras et al., 2007; Delfino et al., 2008), and *Salamandrina* and plethodontid salamanders among the amphibians that are tied to

humid terrestrial, non lentic or lotic, niches (Delfino, 2002; Venczel and Sanchiz, 2005; Delfino et al., 2006; Delfino and Sala, 2007). Particularly interesting is the case of the fully terrestrial plethodontid salamanders of the genus *Hydromantes* that have in the Italian biogeographic region the only Palaearctic representatives with their sister taxon living in Korea (Buckley et al., 2010). These lungless salamanders are tied to environments with high environmental humidity that allow gas exchanges through their skin, but the fact that they have interstitial habits could imply the influence of factors that go beyond those that controlled the survival of plants. It should also be mentioned that the last European occurrence of the frog genus *Latonia*, known since the Oligocene, is the one of Pietrafitta (Delfino, 2002; Rage and Rocek, 2003), a Calabrian site in Central Italy (Martinetto et al., 2014) and that this genus, described on the basis of fossil material and long considered extinct, was recently found alive in Israel (Biton et al., 2013).

5. Discussion

Depending on the concepts of "physiological uniformitarianism" (Tiffney and Manchester, 2001) and deterministic late Cenozoic plant extinctions in Europe (Svenning, 2003) we singled out three groups of plant fossil-species occurring in southern Europe: CTEA, HUTEA, TEWA. The CTEA and HUTEA include several species extinct in Europe, belonging to supraspecific plant taxa with a partly shared modern distribution in East Asia. The HUTEA are the descendants of the “exuberant laurophyllous flora” (Kubitzki and Krutzsch, 1996) growing in the warm temperate belt of southern Laurasia during the Eocene. At this time many taxa now distributed in eastern Asia were present in North America and Europe, but later survived only in the first and, partly, in the second continent. For this reason it would be more appropriate to speak about taxa “conserved in East Asia” rather then “of East Asian affinity”.

Several taxa that toletared cooler conditions (including many CTEA) tended to occupy a higher latitudinal belt during the Eocene and Early-Middle Miocene, and were able to survive both in eastern Asia and eastern North America, but not in Europe (Tiffney and Manchester, 2001; Wen et al., 2010). In fact, the present Asian-American biogeographic disjunction of several plant taxa (*Hamamelis*, *Liquidambar*, *Liriodendron*, *Magnolia*, ecc.) “mostly represents relict distributions of a wider distribution in the Tertiary. It is a product of complex processes such as migration/dispersal, extinction, speciation, vicariance, and perhaps also evolutionary convergence and stasis” (Wen et al., 2010).

Phylogenetic studies based on disjuct eastern Asian-eastern North American living plants (e.g. Magnoliaceae: Nie et al, 2008) pointed out that the divergence times mostly date back to Eocene-Miocene (Wen et al., 2010). The divergence times of extinct European taxa and their extant eastern Asian sister taxa is poorly understood, even if a few recent studies incorporated fossils in the phylogenies (e.g. Xiang et al., 2006; Denk and Grimm, 2009; Zhang et al., 2013; Fritsch et al., 2015).

Despite this lack of information, the available literature is sufficient to explain why it is convenient to the separate the groups CTEA, HUTEA and TEWA: during the Eocene and/or Early-Middle Miocene, under equable climatic conditions (Wing and Greenwood, 1993; Zachos et al., 2001; Tiffney and Manchester, 2001; Grímsson et al., 2015), a north-south differentiation of the flora (and vegetation) was already present, so that the boreal regions were covered by cool-tolerant taxa (e.g. *Fagus, Juglans*: Aradhya et al., 2007; Denk and Grimm, 2009), some of which can be classified as CTEA (e.g. *Chamaecyparis*: Liu et al., 2009), and the middle latitudes were covered by more thermophilous taxa, including many HUTEA and TEWA, not adapted to regular and severe frost (e.g. *Cinnamomum*, *Engelhardia*, *Mastixia*, *Ocotea*, *Sideroxylon*, *Symplocos* sect. *Lodhra*, *Tetraclinis*, *Toddalia*, etc.). However, also several CTEA grew in these warm mid-latitude forests: in fact, even if we indicated the CTEA as a group of cool-tolerant plants, this applies only to the supraspecific taxa, and several CTEA species were probably as thermophilous as the HUTEA (see above the example of *Magnolia*). This hypothesis is corroborated by the observation that several

660 CTEA species display a HUTEA-like pattern of disappearance in Italy (see CTEA2 and CTEA3 in
661 Fig. 9), which could suggest a similar thermophilous attitude.
662 The analysis of the percentage of HUTEA species in some well-dated early Pliocene to early
663 Pleistocene carpofloras of Italy (excluded those newly analysed here) provided an interesting
664 picture: values above 15% in the Zanclean, above 7% in the Piacenzian, 2-0% percent in the
665 Gelasian and invariably 0% in the Calabrian (Figs 8, 9). Furthermore, an analysis of the early
666 Pleistocene carpofloras of Europe Table 2) showed that most of them do not contain HUTEA, apart
667 *Eucommia* and possibly *Glyptostrobus* and *Symplocos* sect. *Lodhra* in the Colchis refugial area
668 (Chochieva, 1975; Shatilova et al., 2014). Thus, our new record of the San Lazzaro section is of
669 particular relevance, because for the first time an assemblage containing a very high percentage
670 (50%) of HUTEA is documented in European sediments independently dated to the early
671 Pleistocene. This is in agreement with a previous record (Martinetto, 2001a) of the same species
672 occurring at San Lazzaro (*Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana*) in the
673 continental sediments of another early Pleistocene site of central Italy, Cava Toppetti II, even if in
674 this second site the percentage of HUTEA is definitely lower (7%). The reconsideration of the
675 stratigraphic data, in particular the biochronologic indications of continental molluscs and
676 vertebrates, allows us to confirm a Gelasian age for the Cava Toppetti II section, the flora-bearing
677 layer being most likely deposited between 2.1 and 1.9 Ma. The independent age assignments of the
678 Cava Toppetti II and San Lazzaro sections point to a time-correlation of the warm and humid
679 HUTEA-bearing phase detected in both of them. The combined record of the two sections is
680 fundamental to prove that the three above-mentioned HUTEA species actually survived in central
681 Italy after the Pliocene/Pleistocene boundary, and to rule out the suspect that the occurrence of their
682 carpological remains in the marine San Lazzaro section could be due to the reworking from older
683 (Pliocene) sediments (Martinetto et al., 2015).
684 Even if most of the HUTEA documented in the Pliocene (Fig. 9) are not yet reported in the early
685 Pleistocene, it may be argued that this is a bias due to the scarcity of records. Indeed, the proved
686 occurrence in the early Pleistocene of such thermophilous and humidity-requiring plants as
687 *Symplocos* sect. *Lodhra* and *Toddalia* suggests the possibility that also other HUTEA would have
688 crossed the Pliocene/Pleistocene boundary. Chiarini et al. (2009) reported fruits of *Engelhardia*
689 from a poorly dated section that could be of early Pleistocene age. Pollen data suggest the
690 persistence of *Engelhardia* in central Italy until the Middle Pleistocene (Biltekin et al., in press) and
691 in Spain till to the early Pleistocene (Postigo-Mijarra et al., 2009). These late occurrences are in
692 agreement with the suggestion by Kvaček (2007) that the European *Engelhardia* is an extinct
693 phylogenetic clade that was more cool-tolerant than the extant Asian species, and possibly it should
694 be excluded from the HUTEA in future analyses.
695 The possible late occurrence of a few potential HUTEA is also implicit in other South European
696 palynological assemblages (Tsedakis et al., 2006; Postigo-Mijarra et al., 2009; Bertini, 2010; Magri,
697 2010; Popescu et al., 2010; Orain et al., 2013; Shatilova et al., 2014; Biltekin et al., in press;
698 Combourieu-Nebout et al., 2015), reporting *Eucommia*, *Symplocos* and "Taxodiaceae" pollen up to
699 the Calabrian, and in some areas to the Middle Pleistocene (Shatilova et al., 2014; Biltekin et al., in
700 press) or Holocene ("Taxodiaceae": Biltekin et al., in press). However, the identification at genus
701 (for the "Taxodiaceae") or section level (for *Symplocos*), which is necessary for the assignement to
702 the CTEA or HUTEA, is mostly not provided in such works (except Biltekin et al., in press).
703 To our knowledge the single macrofossil of a HUTEA in the Middle Pleistocene of Europe is a
704 wood of *Amentotaxus* sp. (Follieri, 2010) from central Italy, associated to several taxa that later
705 went extinct in Europe (*Taxodium*, the CTEA *Cephalotaxus* and *Torreya*, and the TEWA *Ocotea*).
706 We cannot exclude that central-southern Italy may have offered a refugial niche that was warm and
707 wet enough to assure the longer survival of a few HUTEA, in contrast to central Europe. In fact
708 pollen data document the persistence of potential HUTEA ("Taxodiaceae") and humidity-requiring
709 CTEA (*Carya*) till to the Middle Pleistocene in central and southern Italy (Manzi et al., 2011; Magri
710 and Palombo, 2013; Orain et al., 2013; Biltekin et al., in press). However, most of the CTEA have

711 the last macrofossil record (Martinetto, 1999, 2001a; Martinetto et al., 2015) in the time span from
712 1.4 to 0.8 Ma (Fig. 9).
713 Also a simple comparison of the fossil record and the current distribution of the terrestrial
714 ectothermic vertebrates suggests that the Italian biogeographic region acted as a humid refugium. It
715 is actually tempting to associate the history of plants with that of these animals, whose distribution
716 is clearly related to historical variations of temperature and humidity more directly than that of
717 other vertebrates. However, it seems that despite the possibility of identifying a general common
718 trend there are significant differences that are only partly related to the incompleteness of the fossil
719 records of both groups. Conversely, a particularly intriguing argument is the concomitant
720 persistence in the San Lazzaro section of thermophilous terrestrial plants and unexpected (for the
721 early Pleistocene) thermophilous marine benthic taxa, such as *Amphistegina* spp. and
722 *Persististrombus* cf. *coronatus* (Bizzarri and Baldanza, 2006; Harzhauser and Kronenberg, 2008;
723 Monaco et al., 2011).
724 It is well known that the Pliocene is characterized by intense climatic oscillations of increasing
725 amplitude, also at the middle latitudes (De Shepper et al., 2013), with cold pulses at 3.7-3.6 Ma, 3.3
726 Ma (Zanclean/Piacenzian transition) and intense glaciations during late Piacenzian-early Gelasian,
727 at 2.7-2.4 Ma (Zachos et al., 2001; Lisecki and Raymo, 2005; Prescott et al., 2014). The early
728 Pleistocene is characterized by ~40 kyr lower-amplitude glacio-eustatic oscillations (Combourieu-
729 Nebout et al., 2015), terminating in the mid Pleistocene 'climate revolution' with an abrupt shift to
730 ~100 kyr higher-amplitude oscillations in the late Calabrian, between 0.9 and 0.8 Ma (MIS 23 and
731 MIS 22: Muttoni et al., 2011). This event brought a cooler climate during glacial maxima at the
732 middle latitudes (Ravazzi et al., 2005; Bertini, 2010; Muttoni et al., 2011).
733 The above-mentioned climatic crises were probably responsible for terrestrial plant extinctions
734 (Svenning, 2003; Eiserhardt et al., 2015). In the Italian record (Martinetto, 1999, 2001a; Martinetto
735 et al., 2015) the HUTEA still show a very high percentage in correspondence of the late Piacenzian
736 "warm blip" (CQ1 assemblage: 31%), but a marked decrease in the percentage and number of
737 species (Fig. 8) occurs soon after, in the transition from the Piacenzian to the Gelasian. The north
738 Italian plant assemblages formed during the late Piacenzian cooling (Irace et al., 2012) are totally
739 devoid of HUTEA, but this is not the time of their definitive disappearance from Europe. The new
740 record from the independently dated marine section of San Lazzaro and the related continental
741 record from Cava Toppetti II show that at least three species of HUTEA persisted in central Italy in
742 the Gelasian (*Sinomenium cantalense*, *Symplocos casparyi*, *Toddalia rhenana*). Further macrofossil
743 studies in the Calabrian and Middle Pleistocene are needed for a better assessment of the
744 disappearance time of these and other HUTEA species. In parallel, a more precise dating of
745 important fruit and seed bearing sections should be obtained. If the Dunarobba section would be
746 proven to have an early Pleistocene age (Bizzarri et al., 2011; Martinetto et al., 2014), this would
747 imply that at least 8 HUTEA species (20% of the species in Dunarobba's assemblage DC1b)
748 overcome the Plio/Pleistocene boundary in central Italy (Fig. 9), and the warmest Gelasian peaks
749 still had a flora of definite "Pliocene" character. Actually, the evidences provided by continental
750 molluscs and the fruit and seed assemblages (Fig. 9) suggest a Piacenzian (or transitional
751 Piacenzian-Gelasian) age of the Dunarobba deposits, but also in this case we cannot rule out the
752 persistence of Pliocene taxa in a climatic refugium. In fact, uncertainties in the disappearance time
753 from central Italy of several thermophilous and humid requiring organisms still exist, and further
754 data should be collected. As for plants, particular attention should be addressed to southern Italy,
755 where pollen assemblages (Biltekin et al., in press; Combourieu-Nebout et al., 2015) suggest a
756 longer persistence of thermophilous exotic taxa. However, the lack of palaeocarpological
757 investigations in such an area did not permit a verification of the eventual presence of several
758 HUTEA that do not have a recognizable pollen record (Table 1).
759 The new data collected and the use of the new categories HUTEA, CTEA and TEWA allow us to
760 provide a description of the massive late Cenozoic plant extinction in southern Europe, which is
761 more detailed and effective than the previous ones. For example, Rodriguez Sanchez and Arroyo

(2008) recently provided this version of the story: "in the Piacenzian relict genera of the Tethyan flora still coexisted in southern Europe with ancestors of extant Mediterranean taxa. The onset of the Mediterranean climate in the Pliocene, with hot and dry seasons, and the glacial–interglacial cycles of the Quaternary, with recurrent periods of cold and arid conditions, ultimately caused the extinction of many members of the Tethyan Palaeogene flora in Europe and North Africa (Mai, 1989; Svenning, 2003)".

We suggest here a more articulated scenario: during the Miocene the humidity-requiring descendants of both the Palaeotropical ("Tethyan") and Arctotertiary floras coexisted in Europe (Mai, 1989, 1991), and most of them (TEWA excluded) did not develop an adaptation to aridity. A consistent group of plants, namely our HUTEA, also did not adapt to cool climate, whereas in other groups (our CTEA) cool-tolerant forms had been selected in the course of various Cenozoic cool phases (Zachos et al., 2001). The climatic tolerances of the HUTEA, TEWA (e.g. *Ficus*, *Laurus*, *Liquidambar*, *Ocotea*) and likely thermophilous CTEA species (i.e. CTEA2 in Fig. 9) were probably fixed by a selection under globally equable climates in the Eocene-Miocene time span (Mai, 1989; Wing and Greenwood, 1993; Svenning, 2003; Rodriguez Sanchez and Arroyo, 2008; Manchester et al., 2009; Grímsson et al., 2015), when some HUTEA (*Sargentodoxa*, *Sinomenium*) also grew in North America (Manchester et al., 2009), persisting into the Mio/Pliocene transition (Liu and Jacques, 2010).

In southern Europe the HUTEA, TEWA and thermophilous CTEA species still grew together in the same plant communities (see Martinetto and Vassio, 2010; Martinetto et al., 2015) during the Zanclean, Piacenzian and the Gelasian warm peaks, when the climate was favourable for all of them. Later, thanks to their major drought tolerance (Svenning, 2003; Grimm and Denk, 2012; Utescher and Mosbrugger, 2015), the TEWA found some relatively warm refuges in the Mediterranean (*Coriaria*, *Laurus*, *Liquidambar*, *Olea*, *Styrax*, *Tetraclinis*), North Africa (*Laurus*, *Olea*, *Tetraclinis* and, possibly, *Morella*, *Ocotea*, *Sideroxylon*, *Visnea*) and West Asia (*Olea*, *Sideroxylon*). Some TEWA are today conserved in Macaronesia (*Morella*, *Ocotea*, *Sideroxylon*, *Visnea*) but their arrival there could be as recent as Pleistocene (Kondrasov et al., 2015).

Conversely, the HUTEA did not manage to adapt either to the dry and cool European conditions (Manzi et al., 2011) or to the too dry North African-East Asian ones and survived only in East Asia; just a few of them also survived in wet parts of tropical Africa (e.g. *Toddalia*) and/or America (e.g. *Meliosma* subgen. *Kingsbouroghia*, *Sassafras*, *Saurauia*).

As for the chronology of the disappearance, the Italian record would suggest that the HUTEA were constantly present in the Zanclean-Piacenzian flora of southern Europe, had a small retreat at the Zanclean-Piacenzian transition, possibly affecting four species of HUTEA (Fig. 9), and a larger one at the Piacenzian-Gelasian transition (18 species of HUTEA: Fig. 9); three species of HUTEA (*Toddalia latisiliquata*, *T. rhenana*, *Sinomenium cantalense*) seem to disappear at the Gelasian/Calabrian transition, and there is poor evidence in Italy for the few HUTEA which survived in the Calabrian, even if at least two HUTEA species (*Glyptostrobus europaeus* and *Symplocos casparyi*) were still present during the Calabrian in the Colchidian refugium (Chochieva, 1975). *Engelhardia* and *Eucommia* still occurred in the Calabrian of Italy and Spain (Postigo-Mijarra et al., 2009; Bertini, 2010; Biltekin et al., in press; Martinetto in press PalB); the last southern European macrofossil record of an HUTEA which is presently known is that of *Amentotaxus* sp. in the Middle Pleistocene of central Italy (Follieri, 2010).

Similarly to the HUTEA, also the CTEA did not tolerate dry conditions (Svenning, 2003), but a few ones (*Carya*, *Tsuga*) still survived in the Middle Pleistocene of central-southern Italy (Magri, 2010), Turkey (Biltekin et al., in press) and the Balkan (Tsedakis et al., 2006; Biltekin et al., in press) and Iberian (Postigo-Mijarra et al., 2009) peninsulas, due to the presence of refugia (Combourieu-Nebout et al., 2015) which were humid enough, as demonstrated by the continuous presence of the draught-intolerant *Fagus* until today (Magri, 2008). *Parrotia*, *Pterocarya* and *Zelkova*, which had climatic requirements similar to the CTEA, survived until the present around the Black and Caspian

812 seas (*Zelkova* also in the Mediterranean). Another plant extinct in Europe, *Cedrus,* has particular
813 requirements and histories (Magri, 2012; Su et al., 2013; Biltekin et al., in press).
814 As a whole the carpological data, in connection with the abundant pollen data available, testify that
815 in the late Piacenzian-Middle Pleistocene interval at least 70 plant species (Table 1), including
816 HUTEA (Fig. 9), CTEA (Fig. 9, Table 1) and TEWA (Martinetto et al., 2015), disappeared from the
817 fossil record. However, such a disappearance is not readily interpretable as extinction. By
818 comparing our results with those of Bertoldi et al. (1994), Martinetto (1999, 2001a), Martinetto et
819 al. (2007) and Bertini (2010) it is apparent that the rapidly increasing fossil evidence provided by
820 the Italian carpological and pollen records determined a progressive shift of the last occurrence data
821 of several taxa (e.g.: *Liriodendron*, *Magnolia*, *Sinomenium*, *Symplocos*, *Toddalia*), and there is still
822 space for further changes based on new fossil evidence. We propose that, based on the present
823 evidence, only the concomitant disappearance events of several species, such as the HUTEA2 +
824 CTEA2 (Fig. 9), should be considered as reliably assessed. These concern only two main phases:
825 The Piacenzian/Gelasian transition (main crisis of the HUTEA2 and CTEA2) and the late
826 Calabrian/Middle Pleistocene (main crisis of the CTEA4, last occurrence of the HUTEA
827 *Amentotaxus*). The disappearance events of plant macrofossils at the Zanclean/Piacenzian transition
828 (a few HUTEA1) and Gelasian/Calabrian transition (a few HUTEA3 and CTEA3) appear of minor
829 scale, as also confirmed by the relatively continuous pollen records (Tzedakis et al., 2006; Postigo-
830 Mijarra et al., 2009; Bertini, 2010; Magri, 2010; Orain et al., 2013; Shatilova et al., 2014; Biltekin
831 et al., in press; Combourieu-Nebout et al., 2015). These last events are not univocally interpretable
832 as extinctions, since the taxa which seem to disappear could have become silent for the macrofossil
833 record, though perhaps still present in small relict niches, as suggested by the late occurrence of
834 *Eurya* cf. *stigmosa* (CTEA), *Glyptostrobys europaeus* (HUTEA) and *Symplocos casparyi* (HUTEA)
835 in the Calabrian of the Colchis refugium (Chochieva, 1975; Mai and Martinetto, 2006) and also of
836 *Amentotaxus* (HUTEA), *Cephalotaxus* (CTEA) and *Torreya* (CTEA) in the Middle Pleistocene of
837 central Italy (Follieri, 2010).
838
839 6. Conclusions
840 New data on early Pleistocene fossil fruit and seed assemblages from Italy allowed us to detect
841 several extinct taxa that commonly went unnoticed in pollen analyses. The combined analysis of
842 Pliocene and early Pleistocene occurrence data provided a detailed picture of the reduction of plant
843 diversity in southern Europe. The possible explanation of the causes of plant extinction requires an
844 excursion into deeper times: Several Neogene plants were mainly adapted to grow in thermophilous
845 mesic forests, whose consistent water supply was guaranteed by atmospheric humidity more than
846 groundwater. The climate deterioration of the Plio-Pleistocene cancelled the ecological space of
847 growth of most thermophilous and humidity-requiring taxa. Provided that habitat shift occurred
848 very rarely, most taxa did not manage to adapt to the harsh conditions either from 2.7 to 2.4 Ma or
849 from 1.0 to 0.3 Ma, and went extinct. The chance to avoid extinction was not only a question of
850 temperature, but a combination of this with humidity requirements. Southern Europe became
851 extremely dry during the Pleistocene glacials and those plants requiring both higher temperature
852 and consistent water supply had no chance to find a niche to survive, if not adapted to live along
853 rivers (*Liquidambar*, *Parrotia*, *Platanus*, *Pterocarya*). A few humidity-requiring plants that had
854 already developed an adaptation to cold climate in the Oligocene or Miocene, like *Carya*, could
855 temporarily survive into the Middle Pleistocene also in the inhospitable Europe, possibly in small,
856 not too dry refugia. A similar niche may have saved *Parrotia*, but in the south Caspian area.
857 Our carpological data, in connection to the abundant pollen data available from the literature, testify
858 that the late Zanclean-Middle Pleistocene interval has really been the theatre of a stepwise mass
859 extinction in southern Europe: at least 70 plant species disappeared in two main phases: Piacenzian-
860 Gelasian transition (main crisis of the HUTEA and CTEA2) and late Calabrian-Middle Pleistocene
861 (main crisis of the CTEA4, last occurrence of the HUTEA *Amentotaxus*). The disappearance events
862 at the Zanclean-Piacenzian transition (mostly HUTEA1) and Gelasian/Calabrian transition (a few

HUTEA3 and CTEA3) appear of minor entity and are not univocally interpretable as extinctions. The chronological positions of the two main collective disappearance events coincide with two well-known intervals of major climatic deterioration and support a climatic determinism in the south European extinctions of the investigated plant taxa.

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References

Abbazzi, L., Albianelli, A., Ambrosetti, P., Argenti, P., Basilici, G., Bertini, A., Gentili, S., Masini, F., Napoleone, G., Pontini, M.R., 1997. Paleontological and sedimentological record in Pliocene distal alluvial fan deposits at Cava Toppetti (Todi, Central Italy). Boll. Soc. Paleontol. Ital. 36, 5–22.

Ambrosetti, P., Basilici, G., Capasso-Barbato, L., Carboni, M.G., Di Stefano, G., Esu, D., Gliozzi, E., Petronio, C., Sardella, R., Squazzini, E., 1995a. Il Pleistocene inferiore nel ramo sud occidentale del bacino tiberino (Umbria): aspetti litostratigrafici e biostratigrafici. Il Quaternario 8, 19–36.

Ambrosetti, P., Basilici, G., Ciangherotti, A.D., Codipietro, G., Corona, E., Esu, D., Girotti, O., Lo Monaco, A., Meneghini, M., Paganelli, A., Romagnoli, M., 1995b. La foresta fossile di Dunarobba (Terni, Umbria, Italia centrale): contesto litostratigrafico, sedimentologico, palinologico, dendrocronologico e paleomalacologico. Il Quaternario 8 (2), 465–508.

Aradhya, M.K., Potter, D., Fangyou, G., Simon, C.J., 2007. Molecular phylogeny of *Juglans* (Juglandaceae): a biogeographic perspective. Tree Genet. Genomes 3, 363–378.

Argenti, P., 1999. La biocronologia dei Roditori del Plio-Pleistocene dell'Umbria e l'evoluzione del genere *Apodemus* (Muridae, Rodentia) in Italia). Ph.D. dissertation in Earth Sciences, University of Perugia, 248 pp.

Argenti, P., 2004. Plio-Quaternary mammal fossiliferous sites of Umbria (Central Italy). Geol. Romana 37, 67–78.

Baas, J., 1932. Eine Frühdiluviale Flora im Mainzer Becken. Z. Bot. 25, 289–371.

Baldanza, A., Bertinelli, A., Bizzarri, R., Monaco, P., Parisi, G., 2012. Lungo la costa del Mar Tirreno....due milioni di anni fa. In: Peccerillo, A. (Ed.), L'Ignimbrite di Orvieto-Bagnoregio, pp. 135–159.

Baldanza, A., Bizzarri, R., Famiani, F., Luccioni, I., Pino, P., 2011. Gelasian to Calabrian onland marine record: three case studies in the Mediterranean area. Proceedings of AIQUA Congress: Il Quaternario Italiano - Conoscenze e prospettive (Rome, February 24–25, 2011). Il Quaternario 24, 17–19.

Baldanza, A., Bizzarri, R., Famiani, F., Pasini, G., Garassino, A., De Angeli, A., 2014. The early Pleistocene shallow marine decapod crustaceans community from Fabro Scalo (western Umbria, central Italy): taxonomic inferences and palaeoenvironmental reconstruction. Neues Jahrb. Geol. P.-A. 271 (3), 261–283.

Basilici, G., 1995. Sedimentologia della parte distale di un conoide alluvionale del Pliocene superiore (Bacino Tiberino, Umbria). Il Quaternario 8, 37–52.

914 Basilici, G., 1997. Sedimentary facies in an extensional and deep - lacustrine depositional system:
915 the Pliocene Tiberino Basin, Central Italy. Sediment. Geol. 109, 73–94.
916 Basilici, G., 2000a. Pliocene lacustrine deposits of the Tiberino Basin (Umbria, central Italy). In:
917 Gierlowski-Kordesch, E.H., Kelts, K.R. (Eds.), Lake basins through space and time. AAPG Studies
918 in Geology, vol. 46, pp. 505–514.
919 Basilici, G., 2000b. Floodplain lake deposits on an early Pleistocene alluvial plain (Tiberino Basin,
920 Central Italy). In: Gierlowski-Kordesch, E.H., Kelts, K.R. (Eds.), Lake basins through space and
921 time. AAPG Studies in Geology, vol. 46, pp. 535–542.
922 Basilici, G., Martinetto, E., Pavia, G., Violanti, D., 1997. Paleoenvironmental evolution in the
923 Pliocene marine-coastal succession of Val Chiusella (Ivrea, NW Italy). Boll. Soc. Paleontol. Ital. 36
924 (1–2), 23–52.
925 Bellucci, L., Bona, F., Corrado, P., Magri, D., Mazzini, I., Parenti, F., Scardia, G., Sardella, R.,
926 2014. Evidence of late Gelasian dispersal of African fauna at Coste San Giacomo (Anagni Basin,
927 central Italy): Early Pleistocene environments and the background of early human occupation in
928 Europe. Quat. Sci. Rev. 96, 72–85.
929 Bertini, A., 2010. Pliocene to Pleistocene palynoflora and vegetation in Italy: State of the art. Quat.
930 Int. 225, 5–24.
931 Bertini, A., 2013. Climate and vegetation in the Upper Valdarno basin (central Italy) as a response
932 to Northern Hemisphere insolation forcing and regional tectonics in the late Pliocene-early
933 Pleistocene. Ital. J. Geosci. 132 (1), 137–148.
934 Bertini, A., Martinetto, E., 2011. Reconstruction of vegetation transects for the Messinian /
935 Piacenzian of Italy by means of comparative analysis of pollen, leaf and carpological records.
936 Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 230–246.
937 Bertoldi, R., Martinetto E., 1995. Ricerche paleobotaniche (palinologiche e paleocarpologiche) sulla
938 successione "villafranchiana" del Rio Ca' Viettone. Il Quaternario 8 (2), 403–422.
939 Bertoldi, R., Binotti, A., Castello F., 1994. *Reevesia* and *Itea* in the pollen flora of the Upper
940 Neogene continental deposit at Sarzana (lower Magra valley, Northern Italy). Rev. Palaeobot.
941 Palynol. 80 (1–2), 159–172.
942 Biltekin, D., Popescu S.M., Suc, J.P., Quézel, P., Jiménez-Moreno, G., Yavuz, N., Çağatay, M.N.,
943 in press. Anatolia: a long-time plant refuge area documented by pollen records over the last 23
944 Million years. Rev. Palaeobot. Palynol.
945 Biton, R., Geffen, E., Vences, M., Cohen, O., Bailon, S., Rabinovich, R., Malka, Y., Oron, T.,
946 Boistel, R., Brumfeld, V., Gafny, S., 2013. The rediscovered Hula painted frog is a living fossil.
947 Nat. Commun. 4, 1959. DOI: 10.1038/ncomms2959
948 Bizzarri, R., Baldanza, A., 2006. On the meaning of the *Amphistegina* levels in the Plio –
949 Pleistocene of the Orvieto area (Central Italy). In: Coccioni, R., Marsili A. (Eds.), Proceedings of
950 the Second and Third Italian Meetings on Environmental Micropaleontology. Grzybowski
951 Foundation Spec. Publ., vol. 11, pp. 13–20.
952 Bizzarri, R., Baldanza, A., 2009. Plio-Pleistocene deltaic deposits in the Città della Pieve area
953 (western Umbria, central Italy): facies analysis and inferred relations with the South Chiana Valley
954 fluvial deposits. Il Quaternario 22 (2), 127–138.
955 Bizzarri, R., Albianelli, A., Argenti, P. Baldanza, A., Colacicchi, R., Napoleone, G., 2011. The
956 latest continental filling of Valle Umbra (Tiber Basin, central Italy) dated to one million years ago
957 by magnetostratigraphy. Il Quaternario 24 (1), 51–65.
958 Bizzarri, R., Rosso, A., Famiani, F., Baldanza, A., 2015. Lunulite bryozoans from Early Pleistocene
959 deposits of SW Umbria (Italy): sedimentological and paleoecological inferences. Facies (available
960 on line), doi: 10.1007/s10347-014-0420-6.
961 Bown, P.R., Young, J.R., 1998. Techniques. In: Bown, P.R. (Ed.), Nannofossil biostratigraphy.
962 Kluwer Academic Publishing, The Netherlands, pp. 17–28.
963 Bruch, A., Zhilin, S.G., 2006. Early Miocene climate of Central Eurasia - Evidence from
964 Aquitanian floras of Kazakhstan. Palaeogeogr. Palaeoclimatol. Palaeoecol. 248 (1–2), 32–48.

965 Bruch, A.A., Utescher, T., Mosbrugger, V., 2011. Precipitation patterns in the Miocene of Central
966 Europe and the development of continentality. Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 202–
967 211.
968 Buckley, D., Wake, M.H., Wake, D.B., 2010. Comparative skull osteology of *Karsenia koreana*
969 (Amphibia, Caudata, Plethodontidae). J. Morphol. 271, 533–558.
970 Buzek, C., Kvacek, Z., Holy, F., 1985. Late Pliocene palaeoenvironment and correlation of the
971 Vildstejin floristic complex within Central Europe. Rozpravy Ceskoslovenske Akademie Ved 95
972 (7), 1–72.
973 Cavallo, P., Martinetto, E., 2001. Flore carpologiche del Pliocene di Castelletto Cervo (Biella).
974 Boll. Mus. Reg. Sci. Nat. Torino 18 (2), 277–343.
975 Chiarini, E., Giardini, M., Mattei, M., Porreca, M., Papasodaro, F., Sadori, L., 2009. Plio-
976 Quaternary geological evolution of the high Salto river valley (central Italy): the Marano de' Marsi
977 unit. Il Quaternario 22, 325–344.
978 Cherin, M., Bertè, D.F., Rook, L., Sardella, R., 2013a. *Canis etruscus* (Canidae, Mammalia) and its
979 role in the faunal assemblage from Pantalla (Perugia, central Italy): comparison with the Late
980 Villafranchian large carnivore guild of Italy. Boll. Soc. Paleontol. Ital. 52 (1), 11–18.
981 Cherin, M., Iurino, D.A., Sardella, R., 2013b. New well-preserved material of *Lynx issiodorensis*
982 *valdarnensis* (Felidae, Mammalia) from the Early Pleistocene of Pantalla (central Italy). Boll. Soc.
983 Paleontol. Ital. 52 (2), 103–111.
984 Cherin, M., Bertè, D.F., Rook, L., Sardella, R., 2014a. Re-defining *Canis etruscus* (Canidae,
985 Mammalia): a new look into the evolutionary history of Early Pleistocene dogs resulting from the
986 outstanding fossil record from Pantalla (Italy). J. Mamm. Evol. 21, 95–110.
987 Cherin, M., Iurino, D.A., Sardella, R., Rook, L., 2014b. *Acinonyx pardinensis* (Carnivora, Felidae)
988 from the Early Pleistocene of Pantalla (Italy): predatory behavior and ecological role of the giant
989 Plio-Pleistocene cheetah. Quat. Sci. Rev. 87, 82–97.
990 Chochieva, K.I. 1965. The flora and vegetation of the Chaudian horizon of Guria. "Metsniereba"
991 Publ. H., Tbilisi (in Russian).
992 Chochieva, K.I., 1975. The Khvarbetian fossil forest. "Metsniereba" Publ. H., Tbilisi (in Russian).
993 Ciangherotti, A.D., 1997. Paleoecologic and biostratigraphic analysis of the Middle Pliocene land
994 molluscan faunas from the RDB quarry (Villafrancad'Asti, Piedmont, North-West Italy). Boll. Soc.
995 Paleontol. Ital. 36, 293–301.
996 Ciangherotti, A.D., Esu, D., Girotti, O., 1998. Review of the history of the Late Neogene-Early
997 Quaternary non-marine molluscs of Italy. Mededelingen Nederlandse Instituut Toegepaste
998 Geowetenschappen *TNO* 60, 491–498.
999 Ciangherotti, A., Esu, D., Martinetto, E., Giuntelli, P., 2007. The remarkable Middle Pliocene non-
1000 marine mollusc record from Ceresole d'Alba, Piedmont, north-west Italy: Biochronology,
1001 palaeobiogeography and palaeoecology supported by fossil plants. Geobios 40, 573–587.
1002 Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-X., 2013. The ICS International
1003 Chronostratigraphic Chart. Episodes 36, 199–204.
1004 Combourieu-Nebout, N., Bertini, A., Russo-Ermolli, E., Peyron, O., Klotz, S., Montade, V.,
1005 Fauquette, S., Allen, J., Fusco, F., Goring, S., Huntley, B., Joannin, S., Lebreton, V., Magri, D.,
1006 Martinetto, E., Orain, R., Sadori, L., 2015. Climate Changes in central Mediterranean and Italian
1007 vegetation dynamics since the Pliocene. Rev. Palaeobot. Palynol. DOI:
1008 10.1016/j.revpalbo.2015.03.001
1009 Delfino, M., 2002. Erpetofaune italiane del Neogene e del Quaternario. Ph.D. dissertation in
1010 Palaeontology, University of Modena and Reggio Emilia, 382 pp.
1011 Delfino, M., Sala, B., 2007. Late Pliocene Albanerpetontid (Lissamphibia) from Italy. J. Vertebr.
1012 Paleontol. 27 (3), 716–719.
1013 Delfino, M., Razzetti, E., Salvidio, S., 2005. European plethodontids: palaeontological data and
1014 biogeographical considerations. Atti Museo Civico Storia Naturale "G. Doria" Genova, 97, 45–58.

Delfino, M., Kotsakis, T., Arca, M., Tuveri, C., Pitruzzella, G., Rook, L., 2008. Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. Geodiversitas 30 (3), 641–656.
Denk, T., Grimm, G.W., 2009. The biogeographic history of beech trees. Rev. Palaeobot. Palynol. 158, 83–100.
De Schepper, S., Groeneveld, J., Naafs, B.D.A., Van Renterghem, C., Jan Hennissen, Head, M. J., Louwye, S., Fabian, K., 2013. Northern Hemisphere Glaciation during the Globally Warm Early Late Pliocene. PLOS one, 1–15. PLoS ONE 8(12): e81508. doi:10.1371/journal.pone.0081508
Eiserhardt, W.L., Borchsenius, F., Plum, C.M., Ordonez, A., Svenning, J.-C., 2015. Climate-driven extinctions shape the phylogenetic structure of temperate tree floras. Ecology Letters, early online, doi: 10.1111/ele.12409
Engler, A., 1879–1882. Versuch einer Entwicklungsgeschichte der Pflanzenwelt seit der Tertiaerperiode, Vols 1–2. Engelmann, Leizpig.
Esu, D., Ciangherotti, A., 2004. Palaeoecologic and palaeobiogeographic character of Middle Pliocene non-marine molluscfaunas from North-western Italy. Riv. It. Paleont. Strat. 110, 517–530.
Esu, D., Girotti, O., 1991. Late Pliocene and Pleistocene assemblages of continental molluscs in Italy. A survey. Il Quaternario 4, 137–150.
Esu, D., Girotti, O., 2001. The genus *Prososthenia* Neumayr in Italy (Gastropoda: Prosobranchia: Hydrobiidae). Boll. Soc. Paleontol. Ital. 40, 179–184.
Esu, D., Girotti, O., Kotsakis, T., 1993. Palaeobiogeographical observations on Villafranchian continental molluscs of Italy. Scripta Geologica, spec. vol. 2, pp. 101–119.
Fang, J., Yoda, K., 1989. Climate and vegetation in China II. Distribution of main vegetation types and thermal climate. Ecol. Res. 4, 71-83.
Fang, J., Wang, Z., Tang, Z., 2009. Atlas of Woody Plants in China. Volumes 1 to 3 and index. Higher Education Press, Beijing.
Fang, J., Wang, Z., Tang, Z., 2011. Atlas of Woody Plants in China, distribution and climate, volume 1. Springer, 1972 pp.
Faranda, C., Gliozzi, E., 2008. The ostracod fauna of the Plio-Pleistocene Monte Mario succession (Roma Italy). Boll. Soc. Paleontol. Ital.47, 215–267.
Follieri, M. 2010. Conifer extinction in Quaternary Italian records. Quat. Int. 225 (1), 37–43.
Fritsch, P.W., Manchester, S. R., Stone, R.D., Cruz, B.C., Almeda, F., 2015. Northern Hemisphere origins of the amphi-Pacific tropical plant family Symplocaceae. J. Biogeogr. 42, 891–901. Gavin, D.G., Fitzpatrick, M., Gugger, P.F., et al. 2014. Climate refugia: joint inference from fossil records, species distribution models, and phylogeography. New Phytologist 204 (1), 37–54.
Geissert, F., Gregor, H.J., Mai, D.H., 1990. Die "Saugbaggerflora" eine Frücht- und Samenflora aus dem Grenzbereich Miozän - Pliozän von Sessenheim im Elsass (Frankreich). Documenta naturae 57, 1–208.
Gentili, S., Ambrosetti, P., Argenti, P., 1997. Large carnivore and other mammal fossils from the Early Pleistocene alluvial plain of the Tiberino Basin (Pantalla, central Italy). Preliminary reports. Boll. Soc. Paleontol. Ital. 36, 231–238.
Ghiotto, P., 2010. La carpoflora del bacino lacustre villafranchiano di Steggio (Treviso, Prealpi orientali). Boll. Mus. Reg. Sci. Nat. Torino 27, 3–99.
Gibbard, P.H., Head, M.J., Walker, M.J.C. & The Subcommission On Quaternary Stratigraphy, 2010. Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. J. Quat. Sci. 25 (2), 96–102.
Girotti, O., Capasso Barbato, L., Esu, D., Gliozzi, E., Kotsakis, A., Martinetto, E., Petronio, C., Sardella, R., Squazzini, E., 2003. The section of Torre Picchio (Terni, Umbria, Central Italy): a Villafranchian site rich in Mammals, Molluscs, Ostracods and Plants. Riv. Ital. Paleont. Strat. 109 (1), 77-98.
Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso-Barbato, L., Di Stefano, G., Ficcarelli, G., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C.,

Rook, L., Sala, B., Sardella, R., Torre, D., Zanalda, E., 1997. Biochronology of selected Mammals, Mollusc and Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. Riv. It. Paleont. Strat. 103, 368–388.
Goring, S., Lacourse, T., Pellatt, M.G., Mathewes, R.W., 2013. Pollen assemblage richness does not reflect regional plant species richness: a cautionary tale. J. Ecol. 101, 1137–1145.
Gregor, H.J., 1979. Systematics, Biostratigraphy and Paleoecology of the Genus *Toddalia* Jussieu (Rutaceae) in the European Tertiary. Rev. Palaeobot. Palynol. 28, 311–363.
Gregor, H.J., 1990. Contribution to the Late Neogene and Early Quaternary floral history of the Mediterranean. Rev. Paleobot. Palynol. 62, 309-338.
Grichuk, V. P., 1997. Late Cenozoic changes of flora in extra-tropical Eurasia in the light of paleomagnetic stratigraphy. In: Van Couvering, J. A. (ed.). The Pleistocene Boundary and the Beginning of the Quaternary. Cambridge University Press, Cambridge, pp. 104–113.
Grimm, G.W., Denk, T., 2012. Reliability and resolution of the coexistence approach – a revalidation using modern-day data. Rev. Palaeobot. Palynol. 172, 33–47.
Grímsson, F., Zetter, R., Grimm, G.W., Pedersen, G.K., Pedersen, A.K., Denk T., 2015. Fagaceae pollen from the early Cenozoic of West Greenland: revisiting Engler's and Chaney's Arcto-Tertiary hypotheses. Plant Syst. Evol. 301 (2), 809–832.
Günther, T., Gregor H. J., 1990. Computer-Analyse mitteleuropäischer Frucht- und Samenfloren Europas, Band 2. Documenta Naturae 50 (2), 1–159.
Harzhauser, M., Kronenberg, G.C., 2008. A note on *Strombus coronatus* Defrance, 1827 and *Strombus coronatus* Röding, 1798 (Molluscs: Gastropoda). Veliger 50 (2), 120–128.
Hattori, T., Nakanishi, S., 1985. On the distribution limits of the lucidophyllous forest in the Japanese Archipelago. Bot. Mag. Tokyo 98: 317-333.
Hou, H.Y., 1983. Vegetation of China with reference to its geographical distribution. Annals of the Missouri Botanical Garden 70, 509–548.
Jacques, F. M. B., Shi, G., Wang, W. M., 2013. Neogene zonal vegetation of China and the evolution of the winter monsoon. B. Geosci. 88, 175–193.
Kira, T., 1991. Forest Ecosystems of East and Southeast Asia in a Global Perspective. Ecol. Res. 6, 185–200.
Kirchheimer, F., 1957. Die Laubgewächse der Braunkohlenzeit mit einem kritischen Katalog ihrer Früchte und Samen. W. Knapp Verlag, Halle/Saale, 783 pp.
Kotsakis, T., Delfino, M., Piras, P., 2004. Italian Cenozoic crocodilians: taxa, timing and biogeographic implications. Paleogeogr. Paleoclimatol. Paleoecol. 210, 67–87.
Kovar-Eder, J., Jechorek, H., Kvaček, Z., Parashiv, V., 2008, The Integrated Plant Record: An essential tool for reconstructing Neogene zonal vegetation in Europe. Palaios 23, 97–111.
Kvaček, Z., 2007. Do extant nearest relatives of thermophile European Tertiary elements reliably reflect climatic signal? Palaeog. Palaeoclim. Palaeoecol. 253, 32–40.
Irace, A., Monegato, G., Tema, E., Martinetto, E., Pini, R., Gianolla, D., Bellino, L., 2012. The Pliocene-Pleistocene transition in Southern Piedmont: new data from the Alessandria Basin. INQUA-SEQS 2012: Sassari, Italy, pp. 41–42.
Leone, G., Bonadonna, F., Zanchetta, G., 2000. Stable isotope record in mollusca and pedogenic carbonate from Late Pliocene soils of Central Italy. Palaeogeogr. Palaeoclimatol. Palaeoecol. 163, 115–131.
Lisiecki L.E., Raymo M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic delta O-18 records. Paleoceanogr. 20, 1003.
Liu, Y.-S. (C.), Jacques, F.M.B., 2010. *Sinomenium macrocarpum* sp. nov. (Menispermaceae) from the Miocene–Pliocene transition of Gray, northeast Tennessee, USA. Rev. Palaeobot. Palynol. 159, 112–122.
Liu, Y.-S. (C.), Mohr, B.A.R., Basinger, J.F., 2009. Historical biogeography of the genus *Chamaecyparis* (Cupressaceae, Coniferales) based on its fossil record. Palaeobiodiv. Palaeoenvir. 89, 203–209.

Liu, Y.-S. (C.), Utescher, T., Zhou, Z., Sun, B., 2011. The evolution of Miocene climates in North China: Preliminary results of quantitative reconstructions from plant fossil records. Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 308–317.
Lowe, D.R., 1982. Sediment gravity flows II. Depositional models with special reference to the deposits of high-density turbidity currents. J. Sedim. Petrol. 52 (1), 279–297.
Kondraskov, P., Schütz, N., Schüßler, C., de Sequeira, M.M., Guerra, A.S., Caujapé-Castells, J., Jaén-Molina, R., Marrero-Rodríguez, Á., Koch, M.A., Linder, P., Kovar-Eder, J., Thiv, M., 2015. Biogeography of Mediterranean Hotspot Biodiversity: Re-Evaluating the 'Tertiary Relict' Hypothesis of Macaronesian Laurel Forests. PloS ONE 10(7): e0132091(1-17).
Magri, D., 2008. Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). J. Biogeogr. 35, 450–463.
Magri, D., 2010. Persistence of tree taxa in Europe and Quaternary climate changes. Quat. Int. 219, 145–151.
Magri, D., 2012. Quaternary history of *Cedrus* in southern Europe. Ann. Bot. (Roma) 2012 (2), 57–66.
Magri, D., Palombo, M.R., 2013. Early to Middle Pleistocene dynamics of plant and mammal communities in South West Europe. Quat. Int. 288, 63–72.
Mai, D.H., 1964. Die Mastixioideen-Floren im Tertiär der Oberlausitz. Paläont. Abh. B 2 (1), 1–192.
Mai, D.H., 1970. Subtropische Elemente im europäischen Tertiär I. Die Gattungen *Gironniera, Sarcococca, Illicium, Evodia, Ilex, Mastixia, Symplocos* und *Rehderodendron*. - Paläont. Abh. B, 3 (3–4), 441–503.
Mai, D.H., 1975. Beiträge zur Bestimmung und Nomenklatur fossiler Magnolien. Feddes Repert., 86 (9–10): 559–578.
Mai, D.H., 1989. Development and regional differentiation of the European vegetation during the Tertiary. Plant Syst. Evol. 162, 79–91.
Mai, D.H., 1991. Palaeofloristic changes in Europe and the confirmation of the Arctotertiary-Palaeotropical geofloral concept. Rev. Palaeobot. Palynol. 68, 29–36.
Mai, D.H., 1995a. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer, Jena, 691 pp.
Mai, D.H., 1995b. Paleocarpological investigations in the Villafranchian (Pliocene) of Italy. Boll. Mus. Reg. Sci. Nat. Torino 13 (2), 407-437.
Mai, D.H., Martinetto, E., 2006. A reconsideration of the diversity of *Symplocos* in the European Neogene on the basis of fruit morphology. Rev. Palaeobot. Palynol.140, 1–26.
Mai, D.H., Velitzelos, E., 2007. The fossil flora of Kallithea (Rhodes, Greece) at the Pliocene/Pleistocene boundary. Palaeontographica Abt. B 277, 75–99.
Mai, D.H., Walther, H., 1988. Die pliozänen Floren von Thüringen Deutsche Demokratische Republik. Quartärpaläont. 7, 55–297.
Manchester, S.R, Chen, Z.D., Lu, A.M., Uemura, K., 2009. Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. J. Syst. Evol. 47 (1), 1–42.
Manganelli, G., Giusti, F., 2000. The gastrocoptids of the Fossil Forest of Dunarobba (central Italy) and a preliminary revision of the European Tertiary nominal species of *Albinula* and *Vertigopsis* (Gastropoda Pulmonata: Gastrocoptidae). Boll. Soc. Paleontol. Ital. 39 (1), 55–82.
Manganelli, G., Delle Cave, L., Giusti, F., 1989. Notulae Malacologicae, XLII. Strobilopsidae (Gastropoda, Pulmonata), a family new to the Villafranchian land snail fauna of Apenninic Italy. Basteria 53, 3–13.
Manganelli, G., Giusti, F., Delle Cave, L., 1990. Notulae Malacologicae, XLVIII. Lauriinae (Gastropoda: Pulmonata, Orculidae/Pupillidae) from the Villafranchian of the peninsular Italy. Basteria 54, 87–103.

1166 Manganelli, G., Benocci, A., Esu, D., Giusti, F., 2008. *Staurodon cianfanellianus* n. sp.
1167 (Gastropoda Pulmonata), a new nesopupinevertiginid snail from the Middle-Late Pliocene Fossil
1168 Forest of Dunarobba (central Italy). Boll. Soc. Paleontol. Ital. 47, 211–214.
1169 Manzi, G., Magri, D., Palombo, M.R., 2011. Early-Middle Pleistocene environmental changes and
1170 human evolution in the Italian peninsula. Quat. Sci. Rev. 30, 1420–1438.
1171 Martinetto, E., 1994. Analisi paleocarpologica dei depositi continentali pliocenici della Stura di
1172 Lanzo. Boll. Mus. Reg. Sci. Nat. Torino 12 (1), 137–172.
1173 Martinetto, E., 1995. Significato cronologico e paleoambientale dei macrofossili vegetali
1174 nell'inquadramento stratigrafico del "Villafranchiano" di alcuni settori del Piemonte (Italia NW).
1175 Ph.D. Thesis, University of Turin, Italy.
1176 Martinetto, E., 1998. East Asian elements in the Plio-Pleistocene floras of Italy. In: Aoluo, Z.,
1177 Sugong, W. (Eds.), Proc. Int. Symp. Floristic Charact. Diversity East Asian Plants. Springer-Verlag,
1178 pp. 71–87.
1179 Martinetto, E., 1999. Chronological framing of Pliocene to Early Pleistocene plant macrofossil
1180 assemblages from northern Italy. Acta Palaeobot. Suppl. 2, 503–511.
1181 Martinetto, E., 2001a. The role of central Italy as a centre of refuge for thermophilous plants in the
1182 late Cenozoic. Acta Palaeobot. 41 (2), 299–319.
1183 Martinetto, E., 2001b. Studies on some exotic elements of the Pliocene floras of Italy. Palaeont.
1184 Abt. B 259, 149–166.
1185 Martinetto, E., 2003. Leaves of terrestrial plants from the shallow marine and transitional Pliocene
1186 deposits of Asti (Piedmont, NW Italy). Boll. Soc. Paleontol. Ital. 42 (1-2), 75-11.
1187 Martinetto, E., 2009. Palaeoenvironmental significance of plant macrofossils from the Piànico
1188 Formation, Middle Pleistocene of Lombardy, North Italy. Quat. Int. 204, 20–30.
1189 Martinetto, E., Scardia, G., Varrone, D., 2007. Magnetobiostratigraphy of the Stura di Lanzo fossil
1190 forest succession (Piedmont, Italy). Riv. Ital. Paleont. Strat. 113 (1), 109-125.
1191 Martinetto, E., Bertini, A., Basilici, G., Baldanza, A., Bizzarri, R., Cherin, M., Gentili, S., Pontini,
1192 M.R., 2014. The plant record of the Dunarobba and Pietrafitta sites in the Plio-Pleistocene
1193 palaeoenvironmental context of central Italy. Alp. Med. Quat. 27 (1), 29–72.
1194 Martinetto, E., Monegato, G., Irace, A., Vaiani, S.C., Vassio, E., 2015. Pliocene and Early
1195 Pleistocene carpological records of terrestrial plants from the southern border of the Po Plain
1196 (northern Italy). Rev. Palaeobot. Palynol., doi:10.1016/j.revpalbo.2014.10.007
1197 Martinetto, E., in press. Challenges to the monographic investigation of the Pliocene and Early
1198 Pleistocene carpofloras of Italy. Palaeontographica Abt. B.
1199 McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen,
1200 P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme van Reine, W.F., Smith, G.F., Wiersema, J.H.,
1201 Turland, N.J. (eds. & comps.), 2012. International Code of Nomenclature for algae, fungi, and
1202 plants (Melbourne Code), adopted by the Eighteenth International Botanical Congress Melbourne,
1203 Australia, July 2011. Koeltz Scientific Books, Königstein, 240 pp.
1204 Momohara, A., 2015. Stages of major floral change in Japan based on macrofossil evidence and
1205 their connection to climate and geomorphological changes since the Pliocene. Quat. Int.,
1206 doi:10.1016/j.quaint.2015.03.008.
1207 Monaco, P., Famiani, F., Bizzarri, R., Baldanza, A., 2011. First documentation of wood borings
1208 (*Teredolites* and insect larvae) in isolated clasts of Early Pleistocene lower shoreface deposits
1209 (Orvieto area, central Italy). Boll. Soc. Paleontol. Ital. 50 (1), 55–63.
1210 Muttoni, G., Scardia, G., Kent, D.V., Morsiani, E., Tremolada, F., Cremaschi, M., Peretto, C., 2011.
1211 First dated human occupation of Italy at ~0.85 Ma during the late Early Pleistocene climate
1212 transition. Earth Planet. Sc. Lett. 307, 241–252.
1213 Muttoni, G., Kent, D.V., Scardia, G., Monesi, E., 2014. Migration of hominins with megaherbivores
1214 into Europe via the Danube-Po gateway in the late Matuyama climate revolution. Riv. It. Paleont.
1215 Strat. 120 (3), 351–365.

1216 Napoleone, G., Albianelli, A., Azzaroli, A., Bertini, A., Magi, M., Mazzini, M., 2003. Calibration
1217 of the Upper Valdarno Basin to the Plio-Pleistocene for correlating the Apennine continental
1218 sequences. Il Quaternario 16 (1Bis), 131–166.
1219 Napoleone, G., Albianelli, A., Fischer, A.G., 2004. Magnetic susceptibility cycles in Upper
1220 Pliocene lacustrine deposits of the Northern Apennines, Italy. In: Cyclostratigraphy: Approaches
1221 and Case Histories. SEPM Spec. Publ., vol. 81, pp. 263–274.
1222 Nemec, W., Steel, R.J., 1984. Alluvial and coastal conglomerates: their significant features and
1223 some comments on gravelly mass - flow deposit. In: Koster, E.H., Steel, R.J. (Eds.), Sedimentology
1224 of gravels and conglomerates. CSPG Mem., vol. 10, pp. 1–31.
1225 Orain, R., Lebreton, V., Russo Ermolli, E., Combourieu-Nebout, N., Sémah, A.M., 2013. *Carya* as
1226 marker for tree refuges in southern Italy (Boiano basin) at the Middle Pleistocene. Palaeogeogr.
1227 Palaeoclimatol. Palaeoecol. 369, 295–302.
1228 Petronio, C., Argenti, P., Caloi, C., Esu, D., Girotti, O., Sardella, R., 2003. Updating Villafranchian
1229 mollusc and mammal faunas in Umbria and Latium (Central Italy). Geol. Romana 36, 369–387.
1230 Piras, P., Delfino, M., Del Favero, L., Kotsakis, T., 2007. Phylogenetic position of the crocodylian
1231 *Megadontosuchus arduini* (de Zigno, 1880) and tomistomine palaeobiogeography. Acta Pal. Pol. 52
1232 (2), 315–328.
1233 Pontini, M.R., 1997. Analisi palinologica e interpretazione paleo climatica dei depositi continentali
1234 del Bacino Tiberino (Umbria, Italia). Ph.D. dissertation in Palaeontology, University of Perugia,
1235 134 p.
1236 Pontini, M.R., Albianelli, A., Basilici, G., Bertini, A., Napoleone, G., 2002. Palynology and
1237 magnetostratigraphy of the Middle - Late Pliocene lacustrine sequence in the Tiberino basin (central
1238 Italy). Boll. Soc. Geol. It., Vol. Spec. 1 (2), pp. 467–472.
1239 Popescu, S.M., Biltekin, D., Winter, H., Suc, J.P., Melinte-Dobrinescu, M.C., Klotz, S.,
1240 Combourieu-Nebout, N., Rabineau, M., Clauzon, G., Deaconu, F., 2010. Pliocene and Lower
1241 Pleistocene vegetation and climate changes at the European scale: Long pollen records and
1242 climatostratigraphy. Quat. Int. 219, 152–167.
1243 Popova, S., Utescher, T., Gromyko, D.V., Bruch, A.A., Mosbrugger, V., 2012. Palaeoclimate
1244 evolution in the Cenozoic of Siberia — evidence from fruit and seed floras. Turk. J. Earth Sci. 21,
1245 315–334.
1246 Postigo-Mijarra, J.M., Barrón, E., Manzaneque, F., Morla, C., 2009. Floristic changes in the Iberian
1247 Peninsula and Balearic Islands during the Cenozoic. J. Biogeogr. 36 (11), 2025–2043.
1248 Prescott, C.L., Haywood, A. M., Dolan, A.M., Hunter, S.J., Pope, J.O, Pickering, S.J., 2014.
1249 Assessing orbitally-forced interglacial climate variability during the mid-Pliocene Warm Period.
1250 Earth Planet. Sci. Lett. 400, 261–271.
1251 Qian, H., Wang, S., He, J.S., Zhang, J., Wang, L., Wang, X., Guo, K., 2006. Phytogeographical
1252 analysis of seed plant genera in China. Ann. Bot-London 98, 1073–1084
1253 Raffi, I., 2002. Revision of the early – middle Pleistocene calcareous nannofossil biochronology
1254 (1.75–0.85 Ma). Mar. Micropaleontol. 45, 25–55.
1255 Rage, J.C., Rocek, Z., 2003. Evolution of anuran assemblages in the Tertiary and Quaternary of
1256 Europe, in the context of palaeoclimate and palaeogeography. Amphib. Reptil. 24, 133–250.
1257 Ravazzi, C., Pini, R., Breda, M., Martinetto, E., Mattoni, G., Chiesa, S., Confortini, F., Egli, R.,
1258 2005. The lacustrine deposits of Fornaci di Ranica (late Early Pleistocene, Italian Pre-Alps):
1259 stratigraphy, palaeoenvironment and geological evolution. Quat. Int. 131, 35–58.
1260 Reid, C., Reid, E.M., 1915. The Pliocene floras of the Dutch- Prussian border. Meded. Rijksopsp.
1261 Delfst. 6, 1–178.
1262 Reid, E.M., 1920. Recherches sur quelques graines pliocénes du Pont-de-Gail (Cantal). Bull. Soc.
1263 Geol. France, ser. IV, 20, 48–87.
1264 Rio, D., Raffi, I., Villa, G., 1990. Pliocene-Pleistocene calcareous nannofossil distribution patterns
1265 in the Western Mediterranean. In: Kastens, K., Mascle, J. (Eds.), Proc. ODP Science Results, Vol.
1266 107, pp. 513–533.

Rodríguez-Sánchez, F., Arroyo, J., 2008. Reconstructing the demise of Tethyan plants: climate-driven range dynamics of *Laurus* since the Pliocene. Global Ecol. Biogeogr. 17, 685–695.
Sala, B., Masini, M., 2007. Late Pliocene and Pleistocene small mammal chronology in the Italian peninsula. Quat. Int. 160, 4–16.
Sardella, R., Angelone, C., Barisone, G., Bedetti, C., Di Canzio, E., Marcolini, F., Squazzini, E., 2003. Italian Plio-Pleistocene mammal biochronology and correlation with marine sequences: three case studies. Il Quaternario 16, 15–20.
Shatilova, I., Rukhadze, L., Kokolashvili, I., 2014. The History of Genus *Juglans* L. on the Territory of Georgia. Bull. Georg. Nat. Acad. Sci. 8(2), 109–115.
Su, T., Liu, Y.S., Jacques, F.M.B., Huang, Y.J., Xing, Y.W., Zhou, Z.K., 2013. The intensification of the East Asian winter monsoon contributed to the disappearance of *Cedrus* (Pinaceae) in southwestern China. Quaternary Research 80, 316–325.
Svenning, J.C., 2003. Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. Ecol. Lett. 6, 646–653.
Szafer, W., 1961. Miocene Flora from Stare Gliwice in Upper Silesia. Prace Geol. Inst. Warszawa 33: 1–205.
Tallis, J.K., 1991. Plant community history. 398 pp., Chapman & Hall, London. Torre, D., Albianelli, A., Azzaroli, A., Ficcarelli, G., Magi, M., Napoleone, G., Sagri, M., 1993. Paleomagnetic calibration of late Villafranchian and mammalian faunas from the upper Valdarno, Central Italy. Mem. Soc. Geol. It. 49, 335–344.
Thomasson, J.R., 1991. Sediment-borne ‘‘seeds’’ from Sand Creek, Northwestern Kansas: taphonomic significance and paleoecological and paleoenvironmental implications. Palaeog. Palaeoclim. Palaeoecol. 85, 213-225.
Torre, D., Albianelli, A., Bertini, A., Ficcarelli, G., Masini, F., Napoleone, G., 1996. Paleomagnetic calibration of Plio- Pleistocene mammal localities in Central Italy. Acta Zool. Crac. 39, 559–570.
Tralau, H., 1963. Asiatic Dycotyledonous affinities in the Cainozoic flora of Europe. K. svenska vetensk. Akad. Handl., Fjärde Ser., 9 (3), 1–84.
Tzedakis, P.C., Hooghiemstra, H., Pälike, H., 2006. The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and longterm vegetation trends. Quat. Sci. Rev. 25, 3416-3430.
Utescher, T., Mosbrugger, V., 2015. The Palaeoflora Database: at http://www.palaeoflora.de [accessed on 26th Jan. 2015]
Utescher, T., Bruch, A.A., Micheels, A., Mosbrugger, V., Popova, S., 2011. Cenozoic climate gradients in Eurasia - a palaeo-perspective on future climate change? Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 351–358.
Utescher, T., Bruch, A.A., Erdei, B., François, L., Ivanov, D., Jacques, F.M.B., Kern, A.K., Liu, Y-S., Mosbrugger, V., Spicer, R.A., 2014. The Coexistence Approach—theoretical background and practical considerations of using plant fossils for climate quantification. Palaeogeogr. Palaeoclimat. Palaeoecol. 410, 58–73.
Vassio, E., Martinetto, E., 2012. Biases in the frequency of fruits and seeds in modern fluvial sediments in northwestern Italy: the key to interpreting analogous fossil assemblages. Palaios 27, 779–797.
Velichkevich, F.Yu., Zastawniak, E., 2003. The Pliocene flora of Kholmech, south-eastern Belarus and its correlation with other Pliocene floras of Europe. Acta Palaeobot. 43, 137–259.
Venczel, M., Sanchíz, B., 2005. A fossil plethodontid salamander from the Middle Miocene of Slovakia (Caudata, Plethodontidae). Amphib. Reptil. 26, 408–411.
Wang, C.-W., 1961. The forests of China with a survey of grassland and desert vegetation. Maria Moors Cabot Foundation Publication, 5. Harvard University, Cambridge, MA.
Wing, S. L., Greenwood, D. R., 1993. Fossils and fossil climate: The case for equable continental interiors in the Eocene. Philos. T. Roy. Soc. B 341, 243–252.

Wolfe, J.A., 1975. Some aspects of plant geography of the northern hemisphere during the late Cretaceous and Tertiary. Ann. Mo. Bot. Gard. 62, 264–279.
Xiang, Q.Y., Thomas, D.T., Zhang, W.H., Manchester, S.R., Murrell, Z., 2006. Species level phylogeny of the dogwood genus *Cornus* (Cornaceae) based on molecular and morphological evidence: implication in taxonomy and Tertiary intercontinental migration. Taxon 55 (1), 9–30.Xing, Y.-W., Utescher, T., Jacques, F.M.B., Tao, S., Liu, Y.-S., Huang, Y.-J., Zhou, Z.-K., 2012. Palaeoclimatic estimation reveals a weakwintermonsoon in southwestern China during the late Miocene: evidence from plant macrofossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 358–360, 19–26.
Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.
Zagwjin, W.H., 1990. Subtropical relicts in the Pliocene flora of Brunssum (The Netherlands). Geol. Mijnbouw 6, 219–225.
Zavala, C., Arcuri, M., Blanco Valiente, L., 2012. The importance of plant remains as diagnostic criteria for the recognition of ancient hyperpycnites. Revue de Paléobiologie, Vol. Spec. 11, pp. 457–469
Zhang, J.B., Li, R.Q., Xiang, X.G., Manchester, S.R., Lin, L., Wang, W., Wen, J., Chen, Z.D., 2013. Integrated fossil and molecular data reveal the biogeographic diversification of the Eastern Asian-Eastern North American disjunct hickory genus (*Carya* Nutt.). PLoS ONE 8 (7), 1–13.
Zhang, J.W., D'Rozario, A., Adams, J.M., Li, Y., Liang, X.Q., Jacques, F.M., Su, T., Zhou, Z.K., 2015. *Sequoia maguanensis*, a new Miocene relative of the coast redwood, *Sequoia sempervirens*, from China: Implications for paleogeography and paleoclimate. American Journal of Botany 102 (1), 103–118.

Figure captions

Figure 1 - Simplified geological scheme for the area of the San Lazzaro, Cava Toppetti and Dunarobba sections.

Figure 2 - Reference lithostratigraphic schemes for the South Valdichiana and Tiberino Basins (modified after Baldanza et al., 2014). 1=San Lazzaro; 2=Cava Toppetti II; 3=Dunarobba.

Figure 3 - Sedimentological/stratigraphic sections in the San Lazzaro area. Location of the biostratigraphic (dots) and carpological (FU3-6) samples is also reported. t*Db*=*Discoaster broweri* LO; b*mG*=medium-sized *Gephyrocapsa* sp. FO (sensu Raffi, 2002). CS = clay, silt; G = gravel.

Figure 4 - Panoramic view of the San Lazzaro quarry. The richest fruit and seed bearing deposit (FU5) was located at the transition from the grey to the yellowish sediments (1/3 above the bottom of the image).

Figure 5 - Detail of a lens of mixed shells and compressed phytodebris at ca. 8 m from the base of the San Lazzaro section (see FU4 in Fig. 3).

Figure 6 - Resumed geological setting, sedimentological interpretation, magnetostratigraphic and biochronological calibration, and fossil record for the Cava Toppetti II site (redrawn after Abbazzi et al., 1997). Original vertebrates taxonomy reported by Abbazzi et al. (1997) is not revised nor further discussed herein.

Figure 7 - Aspect of the deposits with compressed macroscopic plant remains in the Cava Toppetti II section as they appeared in the year 1998. The sampled fruit and seed bearing sediment (consolidated sandy mud, see NJ1 in Fig. 7) is shown in the detail below.

Figure 8 - Histograms of the percentage of HUTEA species in some well-dated early Pliocene to Early Pleistocene floras of Italy (dark grey bars). Records from San Lazzaro, Dunarobba and Cava Toppetti II are also reported (pale grey bars). Numbers indicate the total of HUTEA species in each assemblage. See label explainations and locality data in Table 2.

Figure 9 - Scheme summarizing the chronological distribution of carpological records of selected species in the Pliocene and early Pleistocene of northern-central Italy. The records from all the localities accessed into the CENOFITA database (Martinetto and Vassio, 2010; Martinetto et al.,

2015) are reported, according to data published by Basilici et al. (1997), Bertoldi and Martinetto (1995), Ghiotto (2010), Gregor (1990), Martinetto (1994, 1995, 1999, 2001a, 2001b, 2003, 2009, in press), Martinetto et al. (2015). Both the HUTEA and CTEA have been subsivided in groups according to the chronostratigraphic distribution, in such a way that the numbers 1 to 4 correponds to the Groups 1 to 4 in Martinetto et al. (2015). All of the species referred to the HUTEA and CTEA4 have been reported, whereas for the CTEA2 and CTEA3 only selected examples have been shown. The age range for each species is indicated by black bars for the records originating from reliably dated localities (Martinetto, 1999, 2001a, 2003; Martinetto et al., 2007, 2015): Lugagnano (5.1-4.5 Ma), Canale (4.5-3.8 Ma), Cherasco (4.5-3.8 Ma), Pocapaglia (4.5-3.8 Ma), Breolungi (5.1-3.8 Ma), Morozzo (5.1-3.8 Ma), Sento I (3.8-3.6 Ma), Candelo (4.5-3.6 Ma), Baldichieri-Fornace (3.8-3.3), Roatto (3.3-3.2 Ma), RDB Quarry of Villafranca d'Asti (3.3 to 3.1 Ma), Stura di Lanzo Fossil Forest (3.1-3.0 Ma), Marecchia (3.0-2.9 Ma), San Miniato (3.0-2.8 Ma), Castell'Arquato-Monte Falcone (3.0-2.8 Ma), Meleto (2.9-2.8 Ma), Santa Barbara (2.9-2.7 Ma), Castell'Arquato-Arda-AD3 (2.5-2.4 Ma), Casnigo (2.1-1.9 Ma), Poggio Rosso (ca. 1.9 Ma), Santerno-Codrignano (1.8-1.7 Ma), Leffe 1st browncoal (1.6-1.4 Ma), Stirone-Laurano-LA1 (1.1-1.0 Ma), Enza-EZ38 (1.1-1.0 Ma), Ranica (1.1-1.0 Ma), Oriolo (1.0-0.8 Ma), Stirone-Laurano-LA3 (0.9-0.8 Ma), Pianico-BVC lithostratigraphic unit (0.8-0.7 Ma). Hatched bars indicate records from the following poorly dated localities (see Martinetto, 1999; Martinetto et al., 2015): Ca' Viettone (late Zanclean, possibly 3.8 to 3.6 Ma); Fossano (late Zanclean, possibly 4.0 to 3.6 Ma); Sento II (possibly late Zanclean, 3.8 to 3.6 Ma); Cossato (possibly late Zanclean-early Piacenzian, 3.8 to 3.2 Ma); Front (possibly Piacenzian, 3.3 to 3.0 Ma); Momello-Lanzo (possibly Piacenzian, 3.6 to 3.0 Ma); Castelletto Cervo I (possibly late Piacenzian, 2.8 to 2.6 Ma); Castelletto Cervo II (possibly Gelasian, 2.6 to 2.0 Ma); San Pietro di Ragogna (Gelasian, 2.6 to 1.8 Ma); Buronzo (possibly Gelasian, 2.2 to 1.8 Ma); Steggio (Calabrian, 1.8 to 0.8 Ma). Abbreviations: c = climber; h = herb; MAT = Mean Annual Temperature; Mes = Messinian; MP = Middle Pleistocene; NLR = Nearest Living Relative; s = shrub; t = tree.

Table 1 - Mean Annual Temperature lower threshold values for modern plant genera or subgeneric taxa extinct in Europe ("exotic"), according to the Paleoflora database (PFDB, Utescher and Mosbrugger, 2015), the GrimClim database (CG, Grimm and Denk, 2012), and to different literature sources listed in Appendix 1 (Alternative MATmin). The list is limited to taxa of the HUTEA and CTEA categories with a proved occurrence in the late Cenozoic of Italy, selected as a representative territory for the evaluation of the southern European floral change.

Table 2 - List of the reference localities selected for the calculation of HUTEA species percentage reported in Fig. 8.

Table 3 - Occurrence of HUTEA and CTEA genera in the main Early Pleistocene carpofloras of Europe.

Table 4 - List of the carpological taxa identified in four sediment bulk samples from the San Lazzaro section, see Fig. 3. In brackets the number of specimens for each species.